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PREDATION BY DRAGONFLIES (ODONATA; ANISOPTERA)

by

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA

APRIL 1963

ABSTRACT

The prey, predatory apparatus, and predatory behaviour of dragonfly larvae and adults are described. The structures that are important in prey capture are studied in detail as an aid to understanding the kinds of food that are eaten and the way in which this food is caught. The natural food of pond-dwelling larvae has been studied by analysing the contents of faecal pellets, and comparisons are made between different species, different sizes of larvae, different habitats, and different times of year. Dragonfly larvae are general animal feeders and will attack a wide range of animal life. The composition of their food in nature is affected by a complex of factors including the relative abundance of different prey in the environment, the size and habits of this prey, and the ease with which it is caught and devoured. The prey of adult dragonflies has been studied by gut content analysis and, in this area, is found to consist mainly of small Diptera. Relatively little diminution in the numbers of adult mosquitoes can be expected to occur as a result of dragonfly predation, due to the different conditions required for flight by dragonflies and mosquitoes. Dragonfly larvae generally use speed to catch prey from ambush. In the detection of prey certain species depend mainly on visual stimuli, of which size and movement are the most important. Other species detect prey by tactile stimulation. There is no chemical sampling as a preliminary to the strike, but gustatory sensilla on the

epipharynx probably test food after capture. The behaviour patterns leading up to the strike and the timing and details of labial extension are described. As adults, certain species hunt on the wing whilst others wait in ambush on perches, but all use their legs to take prey in flight. Adults respond at first to movement and size of prey, but its shape probably determines whether or not it is captured. The feeding and sexual phases of behaviour are generally temporally and spatially separated. The evolution of predatory behaviour in larvae and adults is discussed.

ACKNOWLEDGEMENTS

For the supervision of this study and for many helpful suggestions during its preparation, thanks are due to Dr. W.G. Evans and Dr. B. Hocking. I wish also to express my gratitude to the Hughes family, whose hospitality added immeasurably to the enjoyment of the summer of 1962; to Dr. G.E. Ball, whose continued interest has been a great encouragement to me; to Dr. P.S. Corbet for many helpful comments and for the donation of reprints of his own and other authors' works; to Dr. E.M. Walker for kindly confirming my identifications; to Mr. J. Salt for the loan of a motion picture camera and for assistance with attempts to record very high speed pictures of the strike of dragonfly larvae; and to Mr. D.C.D. Happold, discussions with whom have helped to make this study a most pleasant pursuit.

I am grateful to the Canadian Commonwealth Scholarship and Fellowship Committee for a grant that made this work possible.

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"As a zoologist, he wrote as one
of the first to realize that it is what animals do
that makes them interesting, and that the whole of
classical taxonomy and anatomy and physiology is
not an end in itself but an instrument
for the understanding of
their behaviour"

R.J. Pumphrey on
"The forgotten man - Sir John
Lubbock, F.R.S."
(1958)

1. INTRODUCTION

The apparent voracity of dragonflies, the unique modification of the labium of the larva, and the capture of prey by the legs of the adult whilst in flight, have been known for many years. But in spite of this, many questions on dragonfly predation have remained unanswered. What animals form the prey of dragonfly larvae in nature, and are the spectacular captures of large insects by adult dragonflies really typical? What stimuli are important in the release of the strike by larvae and what characters of the prey affect the predatory behaviour of adults? How fast is the larval strike, how accurate is it, and how may it be modified by external and by physiological conditions? How may the predatory behaviour of dragonflies be tied in with their morphology? These are a few of the questions which I have attempted to answer in this study.

Much of the work, particularly that on feeding and adult behaviour, was carried out in the field around Edmonton and in the Flatbush area, 100 miles north of Edmonton. These areas and the habitats therein are described in Section 5.3. Twenty-one species of Anisopteran dragonflies were encountered in the study area and a list of these, with the first dates on which the adults were seen in 1962, is given in Appendix 1. In order to obtain results that were as general as possible the study was not limited to any particular species and most of the 21 species were used at one time or another. Aeshna interrupta

lineata Walker and Libellula quadrimaculata L. were, however, taken as typical examples for most of the morphological work (Sections 2 and 3). Although certain details of predation by dragonflies will be different in other areas and in other species than the ones used here, it is thought that most of the conclusions reached in this study will find general application.

All measurements follow the metric system, temperatures are expressed in degrees centigrade, and times are Mountain Standard Time.

References to important previous work are given in the appropriate places, but mention should be made here of the work of Corbet (1951-1962) whose studies on the biology of dragonflies have provided a basis and a leading-off point for many aspects of this work. The classification of the Odonata follows Fraser (1957).

2. PREDATORY APPARATUS OF DRAGONFLY LARVAE

2.1 The morphology of the head and mouthparts

There are few complete and accurate accounts of the sclerites and muscles of the head and mouthparts of dragonfly larvae. Snodgrass (1954), Asahina (1954), and Short (1955) have given descriptions for Anax junius (Drury), Epiophlebia superstes Selys, and Aeshna cyanea (Müller) respectively, but comparable full descriptions for Libellulid larvae are lacking. The labium of dragonfly larvae has understandably attracted some attention (Brulle, 1833; Butler, 1904; Whedon, 1927; Munscheid, 1933), and certain of its characters may be used taxonomically at least to family level and often further. Corbet (1951) has, however, pointed out the variation that occurs in the setae and spines of the labium of Sympetrum striolatum (Charpentier), thus restricting the use of these structures for identification purposes.

There are two main types of head structure in the Anisoptera; in the Aeshnoid type (Figures 1b and 2b) the head is prognathous and the labium is flat, whilst in the Libelluloid type (Figures 1a and 2a) the head is more nearly hypognathous and the labium is deeply spoon-shaped. Aeshna interrupta lineata and Libellula quadrimaculata are taken as representatives of these two types.

The nomenclature used here follows Snodgrass (1935) for

the most part. The homologies of the distal lobes of the maxilla have been the subject of some controversy in the past, but as Snodgrass (1954) and Short (1955) have pointed out, the arrangement of the muscles precludes the presence of a galea and points to the inner lobe being the lacinia and the outer lobe the palp.

There has also been some confusion over the terminology of the parts of the labium, for some authors have insisted on using the terms 'mentum' and 'submentum' for the sclerites of the prelabium and postlabium respectively. Corbet (1953) has drawn attention to this, and has proposed the use of the terms 'prementum' and 'postmentum' in accordance with Snodgrass's (1935) definition. The terminology for the labial muscles follows Munscheid (1933).

a. Aeshna interrupta lineata

The head capsule (Figure 3) is basically similar to that of a typical orthopteroid, but several features are associated with the structure of the labium and the method of prey capture. The head is prognathous and flattened dorso-ventrally, so that the labium is brought well forward and, at rest, is applied closely to the other mouthparts. The compound eyes are large and cover much of the front and sides of the head, especially in later instars, and consequently there is a reduction of the genae above, in front, and below the eyes. Lew (1933) has described the development of the eyes during the larval stages of Aeshna umbrosa Walker.

The coronal suture (cs) is well defined and branches anteriorly into the postfrontal sutures (pfs) which run between the compound eyes (ce). True frontal sutures are absent. Three dorsal areas of pigmentation (oc) on the vertex (vx) mark the positions of the ocelli. The antennae are seven segmented and are borne on raised areas bordering the frons (fr). Between these areas and the compound eyes are the dorsal tentorial maculae (td). The clypeus (cl) is large and convex and shows evidence of division to anteclypeus and postclypeus.

The posterior wall of the cranium is concave and slopes down to the occipital foramen (for) on all sides. The post-occiput (po) is present as a narrow sclerotized band around the foramen and the posterior tentorial pits (tp) are clearly visible in the bases of the post-occipital suture (pos). There is no distinct division between the occiput (o) and the genae (gen), but the occipital sutures (os) are present from the level of the posterior tentorial pits to the posterior articulations of the mandibles, thus marking off the post-genae (pg) from the genae. The hypostomal border of the cranium and the occipital suture have strong ridges in the region of the posterior mandibular articulation (pam), providing a rigid framework for the support of this area during feeding. The genae are much reduced beneath the compound eyes, but the anterior tentorial pits (ta) can be seen between the eyes and the bases of the mandibles.

The tentorium is π -shaped, forming a strong endoskeleton

for the support of the cranium and providing attachments for certain ventral muscles of the mouthparts. The anterior (aat), posterior (pat), and dorsal arms are all well developed and they widen to their points of attachment with the head capsule. The tentorium provides attachments for ventral muscles of the mandibles, adductors of the cardo and stipes, and extensors of the prementum.

Cook (1944) has described the labrum of an 'unidentified nymph' and Grieve (1937) described the labral muscles of Ischnura verticalis (Say) (Zygoptera) from serial sections. The labrum of Aeshna interrupta lineata (Figure 4) is widest at its free anterior end and is three times as wide as long. The clypeo-labral suture is well defined. Aborally (dorsally) the labrum is well sclerotized and bears forwardly directed setae over the whole surface. The adoral side is more membranous and merges with that of the clypeus. There is an epipharyngeal arrangement of sensilla (sens), but no brushes such as are found in the adult. The tormae are well developed.

The musculature of the labrum consists of three pairs of muscles. The labral compressors (cplr) are a median pair entirely within the labrum and inserted on its dorsal and ventral walls. The anterior labral muscles (mlra) insert medially at the labral base on the dorsal side and originate widely apart on the frons. The posterior labral muscles (mlrp) insert on the tormae at the proximal angles of the labrum on the ventral side, and they originate with the anterior

labral muscles on the frons.

The mandibles (Figure 5) are stout, heavily sclerotized, unsegmented appendages. Four incisor teeth (in) are placed in a single line at the distal end and below these is a molar ridge (mo) with a tooth at each end. This molar ridge is, however, badly named since its function is slicing rather than grinding. The base of the mandible is triangular with anterior, posterior, and inner angles. The articulations are normal; the anterior articulation is with the clypeus and the posterior articulation with the subgena.

There are four muscles, two dorsal and two ventral, which serve the mandible. The dorsal adductor (dad) is very large, originating over a wide area of the posterior wall of the cranium and inserting through an apodeme at the inner angle of the mandibular base. The dorsal abductor (dab) is smaller; it originates on the cranium below the adductor and inserts through an apodeme on the lateral side of the mandibular base, just in front of the posterior articulation. The ventral muscles, which are absent in all higher Pterygotes, are small, and the function of adduction is performed almost entirely by the dorsal muscle. One of the ventral muscles (vmh) originates on the base of the hypopharynx and is inserted inside the cavity of the mandible on the lateral wall, and the other (vmt) originates on the anterior bar of the tentorium and is inserted inside the cavity of the mandible on the posterior wall.

Short (1955) has described the mandible of Aeshna cyanea as being similar to that of the adult, but all adult mandibles studied, including A. cyanea, have a Z-shaped molar area, which is not present in larvae.

The maxilla (Figure 6) has only two distal lobes, the galea being absent. The palp (mxp) is one-segmented and flattened. The lacinia (lc) is broad and bears seven sharp teeth and many long stiff setae.

Each maxilla is served by seven muscles, two of which originate on the cranium between the dorsal mandibular muscles, two originate on the body of the tentorium, and three originate within the stipes. Arising on the cranium are the anterior rotator of the maxilla (rtmxa), which inserts on the base of the cardo (cd), and the cranial flexor of the lacinia (flcc) which inserts on the base of the lacinia. The adductor of the cardo (adcd) and the adductor of the stipes (adst) originate on the body of the tentorium. From the stipes (stp), the stipital flexor of the lacinia (flcs) inserts with the cranial flexor at the lacinial base, the depressor of the palp (dpmp) inserts at the outer angle of the base of the palp, and the levator of the palp (lvmp) inserts on the inner angle of the palpal base. The last two muscles are very small and originate together at the distal end of the stipes.

The labium (Figure 7) of the dragonfly larva is unique; the

sclerites can be homologized but some of the muscles cannot be correlated with those of a generalized insect labium. The postmentum (pom) of Aeshna interrupta lineata is long and flat and the prementum (prm) is spatulate. The labial palps are pincer-like and two-segmented; the first segment is represented by the body of the palp which is projected distally as a blunt 'end-hook' (eh), and the second segment is a sharp, stout 'movable hook' (mh). The labium of Aeshna is devoid of large setae.

Two muscles are inserted at the base of each palp. The abductor of the palp (ablp) originates over a wide area on the dorsal wall of the prementum and inserts through a small apodeme at the outer corner of the base of the palp. The adductor of the labial palp (addlp) is a larger muscle which originates on the ventral wall of the postmentum just proximal to the elbow, and inserts at the inner corner of the palpal base.

There is a single pair of extensor muscles of the prementum (exprm), which originate on the tentorium and are inserted through long apodemes on lever-like extensions of the postmentum past the hinge line.

Three pairs of muscles appear to have flexor functions. The primary flexors of the prementum (l^ofl) are large, originating on the apodeme of the hypopharynx and inserting on the ventral wall of the

prementum just distal to the elbow, whilst the secondary and tertiary flexors are small muscles situated in the elbow and for which no homologues can be found in a generalized labium. The secondary flexors (2^ofl) run directly across the hinge line from the ventral wall of the postmentum to that of the prementum, and the tertiary flexors (3^ofl) originate on the postmentum distal to the secondary flexors, and then run upwards to insert on the lateral walls of the proximal part of the prementum. Snodgrass (1954) believes that this last pair of muscles functions in maintaining a tension on the folds that girdle the palpal adductors. This may be so, but it appears that they also serve a flexor function.

The hypopharynx (Figure 8) arises from the ventral wall of the head directly behind the mouth. It is cushion-like and is narrowest at its base, and setae over its dorsal and lateral sides are directed towards the mouth. The hypopharynx is continuous with the labium through a wide membranous area and in this area the salivary duct opens to a pit (sal) whose sides contain sclerotized bars. These bars are continuations of the lateral walls of the hypopharynx. From the lateral walls is given off a large T-shaped apodeme (Tap), which runs into the base of the labium and is held there by three sets of ligaments. The apodeme in this form is characteristic of dragonfly larvae and is evidently associated with labial extension. At the base of the T-shaped apodeme are inserted the tentorial retractors of the

hypopharynx (rthyp), and the primary flexor muscles of the prementum (1° fl) arise a third of the way down the apodeme from the hypopharynx. The dorsal side of the T-shaped apodeme is grooved and the salivary duct runs in this groove. The hypopharyngeal muscles of the mandibles (vmh) insert on the base of the hypopharynx.

At the base of the hypopharynx on the dorsal side is the suspensorium (susp), a transverse bar which is extended into two dorsal bars which pass up around the primary mouth opening.

b. Libellula quadrimaculata

The head capsule (Figure 9) differs from that of Aeshna interrupta lineata in several important respects. The head is more hypognathous in aspect and is not flattened as in Aeshna. Then the labial palps are developed to such an extent that they cover the whole of the lower and front parts of the head when the labium is at rest, and associated with this is a peculiar development of the eyes that has been described by Lew (1933). Only the dorso-lateral part of the eye is functional in the larva; the lower part, which is covered by the labial mask, remains rudimentary and unpigmented until metamorphosis, when it forms the whole of the lower part of the adult eye and most of the functional larval eye is lost.

The sclerites of the face are arranged so that the labial palps fit around them. A groove between the frons and the clypeus takes the

distal edges of the labial palps, and the clypeus (cl), labrum (lr), mandibles (ma), maxillae, and hypopharynx are normally hidden by the labium. The frons (fr) bulges out above the labial palps and its dorsal border is marked by the attachments of the labral muscles internally. The rudiments of three ocelli can be seen on the vertex (vx), and the coronal (cs) and postfrontal (pfs) sutures are well defined. The antennae are seven-segmented.

The posterior wall of the cranium is not as ~~concave~~ as that of Aeshna, but is similar in all other respects. The posterior articulation of the mandible (pam) is supported by ridges associated with the occipital suture and the hypostoma. The external pits of the posterior and the anterior arms of the tentorium (tp, ta) are disposed in the bases of the postoccipital suture (pos) and just above the anterior articulations of the mandibles respectively. The tentorium (aat, pat) is π -shaped and similar in all respects to that of Aeshna interrupta.

Apart from the labium, the essential features of the mouthparts of Libellula quadrimaculata (Figures 10 to 12) are similar to those of Aeshna. The dorsal muscles of the mandibles are very large and the ventral muscles are small; the maxilla has a sharp-toothed lacinia and lacks a galea; and the hypopharyngeal apodeme is well-developed as a T-shaped rod.

The structure of the labium (Figure 12) of the Libellulid

larva is, however, quite different from that of the Aeshnid in that the labial palps (lp) are greatly enlarged to form a 'mask' which covers the lower parts of the front and sides of the head. The postmentum (pom) is relatively small but the prementum (prm) is large and widens considerably at its distal end. The palps are approximately triangular in shape and, at rest, meet along the length of their inner edges. In this position they form the front and sides of a cup-like arrangement with the prementum. The movable hooks (mh) are present but small, and prey is not necessarily caught with these alone, as it often is by Aeshna. Long palpal and premental setae form a cage-like roof to the cup-shaped labium when it is extended (Figure 13). The muscles of the labium are essentially the same as those present in Aeshna, though the palpal adductors and abductors (addlp, ablp) are especially large. The tentorial extensors of the prementum (exprm) insert through thin apodemes on lever-like extensions of the prementum past the hinge line. The primary flexors of the prementum (1^ofl) originate at the anterior end of the hypopharyngeal apodeme and insert on the latero-ventral walls of the proximal end of the prementum. The secondary flexors (2^ofl) run from their origins on the ventral wall of the postmentum across the hinge line to insert on a dorsal ridge of the prementum. The tertiary flexors (3^ofl) have their origins distal to those of the secondary flexors on the postmentum and insert on the lateral walls of the prementum, as in Aeshna interrupta lineata.

2.2 The action of the mouthparts during feeding

The protraction of the labium is a remarkable mechanical operation which seems especially so when one studies the musculature and finds that this alone cannot produce the forward swing of the postmentum. It would be convenient to assign the function of extending the labium to certain of the available muscles as Amans (1881), Munscheid (1933), and Short (1955) have attempted, but the articulation of the labium with the head is on the anterior side of the postmentum and both the extensor of the prementum and the primary flexor of the prementum pass behind this.

The posterior end of the T-shaped apodeme is fixed to the base of the postmentum and it swings around on its anterior end as the postmentum moves forwards during the strike. The primary flexor of the prementum might be thought to aid in swinging the apodeme down were it not for the fact that such a contraction would work against premental extension, and also, in Libellulids, this muscle is attached at the anterior end of the apodeme and not some way down as in Aeshnids. The retractors of the hypopharynx may, however, aid in producing the desired action of the T-shaped apodeme by pulling the anterior end backwards.

But the more one studies the labial musculature, the more it becomes apparent that the major mechanism of labial extension does not

lie here. The most likely explanation of this action centres around a hydraulic mechanism involving blood pressure, which has been advanced by Snodgrass (1954) and is based on an idea by Amans (1881). Contraction of the muscles of the walls of the thorax and the anterior part of the abdomen are thought to produce a pressure which will act on the labial base to extend the labium. Snodgrass believes that the muscular diaphragm across the abdomen may further aid in generating this pressure and will counteract its backward direction. These theoretical morphological considerations are supported by observations made on the strike. First, the membranous areas behind the labial base and at the articulation between the postmentum and the prementum become inflated as the labium is protracted. Secondly, the anal siphon, formed from the valves of the anus, the paraprocts, the epiproct, and the cerci, closes, at least in Aeshnids, at the instant of the strike. If labial extension is produced by blood pressure the action would presumably be more efficient when the anus is closed so that all of this pressure is directed forwards and none is used to expel water from the colon. And thirdly, the labium can be protracted in a recently dead larva by squeezing the sides of the thorax. This procedure also extends the prementum, but there seems little doubt that in life this is performed by the tentorial extensors of the prementum.

The labial palps open before the labium is extended and they are operated by muscles alone. They are opened by the abductors of the palps and are firmly closed around the prey by the larger

adductors. These latter, in taking their origins on the postmentum, acquire increased effectiveness (Snodgrass, 1954).

Elasticity of the cuticle at the articulations plays a large part in the retraction of the labium. Relaxation of the muscles of the thoracic and abdominal walls relieves the increased pressure and the postmentum swings back to its natural position, whilst the prementum is folded on the postmentum by its three flexor muscles.

The hypopharyngeal apodeme is undoubtedly associated with the protractile nature of the labium. It is firmly fixed in the labial base and it aids in the forward swing and the support of this area during the strike.

Retraction of the labium brings the prey back to the other mouthparts where the mandibles are in a position to cut it up. The mandibles are powerful and heavily sclerotized and their movement is one of strong adduction and weaker abduction in a single plane. The mandibular articulations with the head capsule are well supported and quite rigid, allowing the tips of the mandibles to move only in a plane at right angles to the longitudinal axis of the body, and as one mandible passes over the other the food is crushed and sliced.

If the food is soft the laciniae play no part in breaking it up, but they pass chewed food back over the hypopharynx towards the mouth. Their movement is likely to be a complex one for there are

vertical as well as horizontal components, although basically the movement is one of protraction and retraction in the horizontal-longitudinal plane, with a transverse-horizontal component introduced by the action of the adductors of the cardo and stipes. The maxilla thus traces an oval path. The forward movement is largely produced by the adductor of the cardo, but the retraction is stronger and involves the adductor of the stipes and the cranial flexor of the lacinia. The stipital flexor of the lacinia adds to a further flexing of the lacinia on the stipes. Elasticity of the cuticle is important in certain components of the outward movement of the maxilla, particularly in the extensions of the lacinia and the stipes.

The spines and the stiff setae on the lacinia are well designed for taking both large and small pieces of food which drop from the mandibles, and passing them back to the mouth. When the prey is easily chewed by the mandibles, these and the maxillae work alternately at a steady rate; as the mandibles close the maxillae move forwards, and when the mandibles open and release the chewed pieces of food, the laciniae move inwards and backwards taking the food with them. The rate of chewing depends on many factors including the size of the prey and its activity, and the manner in which it is held by the labial palps. The average rate for 11 Aeshna interrupta lineata larvae, 22 to 29 mm. in length, eating Aedes aegypti L. larvae, was 54 cycles per minute.

If the prey is hard and the mandibles have difficulty breaking it up, the regular activity of the mandibles and maxillae is modified. The action of the maxillae becomes more complex and their cycles of protraction and retraction do not necessarily keep in phase with the action of the mandibles. The movements of the mandibles are irregular, depending on whether they are successful in breaking the cuticle of the prey and the spines of the laciniae are also used from the start in an attempt to tear the food apart. When working on hard parts the laciniae pass food back at irregular intervals, but when soft parts are exposed and chewing becomes easier, there is a return to the regular alternate actions of the mandibles and the maxillae.

The labrum serves to prevent food from floating away and may also function in directing it towards the mandibles, for it is raised and moved forward slightly as the mandibles open and then is lowered and drawn back as the mandibles close. The ventral side of the labrum is the site of possible gustatory sensilla (see Section 4).

Food that is passed back by the maxillae is collected by the backwardly directed setae on the dorsal side of the hypopharynx and is moved towards the mouth. The hypopharynx is probably also the site of sensilla.

During feeding the prey is manipulated by the labium, the mandibles, and the maxillae. The labium is held so that the food is in

the correct position for the mandibles to work on it. This usually demands that the postmentum is swung forward somewhat and presumably controlled blood pressure plays a part here. The prey is often taken by the mandibles whilst the labial palps change their grip, and if the prey is lost and floats upwards a second strike will often be made at it, but pieces that drop from the mouthparts are not usually recovered.

The spatulate prementum of Aeshnids acts as a plate which collects many particles that fall from the mandibles, and these pieces are retrieved by the maxillae at the end of the meal. The cup-like labium of Libelluloids is even more efficient in collecting these food particles, and the arrangement of palpal and premental setae prevents the escape of food upwards.

At the end of a meal the mouthparts are cleaned, particularly the labial palps, which are opened and closed several times to remove all traces of the last meal. The front legs may also be used to clean the labium.

2.3 The morphology of the eyes

The use of the labium as a grasping organ demands good vision. The strike must be released when the prey is in the correct position for capture by the labial palps, and so distance perception must be accurate, and visual acuity should be good if the prey is to

be seen clearly.

The eyes of dragonfly larvae take a variety of forms, but these can be reduced to two basic types. In the Aeshnidae the eyes are large and do not protrude from the head, whilst in the other families the functional eyes are often very small and protruding. Aeshna interrupta lineata and Libellula quadrimaculata have been taken as examples of these two types and sections of the heads of the last larval instars of these species are shown in Figures 14 and 15.

The protuberant nature of the eyes of all but the Aeshnidae may be associated with the small size of the eyes, with the habits of larva, or with the structure of the labium. Although the eyes of the Libellulidae are much smaller than those of the Aeshnidae, the fields of vision are almost the same in both due to greater convexity of the former. The flatter eyes of the Aeshnidae have to cover a much greater area of the head in order to command the same field of view. The Aeshnidae are almost exclusively climbing forms, but other families all contain species that burrow, either in mud or in bottom debris, and these often lie in wait for prey with only the eyes protruding from their camouflage.

The size and shape of the eyes in the Cordulegasteridae and the Libelluloid families is also apparently associated with the shape of the labium, which covers much of the front and sides of the head.

The functional eyes in these forms lie completely above the labial palps and although certain ommatidia are formed below this and are covered by the palps, these visual elements are unpigmented and not functional in the larva (Lew, 1933).

There is a wide angle of binocular vision in front of the head of a dragonfly larva. In Libellula quadrimaculata, the greater part of the eye faces forwards and a large part of the visual field of one eye is also covered by the other eye. The eyes of the last larval instar of Libellula quadrimaculata cover a field of 280° in the horizontal plane and, of this, 112° is seen by both eyes (Figure 15b). In the last larval instar of Aeshna interrupta lineata (Figure 14b) the eyes are more lateral in position and although they cover a greater field of view horizontally (334°), the angle of binocular vision in front of the head (68°) is less than that of L. quadrimaculata. Thus prey in the mid-line in front of the head will always be within the area of binocular vision and distance perception can operate according to the position of the prey on pairs of intersecting ommatidial axes.

In the transverse-vertical plane both species have almost all-round vision. In Aeshna interrupta lineata (Figure 14a) each eye covers a field of about 215° , there being an area of binocular vision of about 68° dorsally in the posterior and middle parts of the eye and ventrally in the more anterior regions. Each eye of Libellula

quadrимaculata (Figure 15a) covers a wider field (223°) and the dorsal overlap of visual fields is 85° .

The resolving power of the insect eye depends on the ommatidial angle. In dragonfly larvae, the ommatidial angle is smallest in the anterior part of the eye, in the region of binocular vision, and it increases posteriorly and dorsally. Consequently, as the predator approaches its prey the latter will become more and more clear as the visual acuity increases with decreasing ommatidial angle. The minimum ommatidial angle in Aeshna interrupta lineata is $1^{\circ}12'$, and that of Libellula quadrимaculata is slightly larger at $1^{\circ}42'$. Baldus (1926) proposed that when the image falls on the parts of the eye with the minimum ommatidial angle the prey is at the correct distance for capture by the labium. In the posterior and dorsal parts of the eye of Aeshna interrupta lineata the ommatidial angle is at a maximum of $3^{\circ}6'$, whilst the same parts of the protruding eyes of Libellula quadrимaculata are very convex and the ommatidia subtend wide angles of up to $7^{\circ}42'$ in these regions.

All of the ommatidia are of the apposition type, suitable for forming sharp images in daylight. It is not known whether pigment migrations occur allowing the formation of super-position images, but dragonfly larvae can detect prey in very dim light.

The larger number of facets and the smaller ommatidial

angles, lead one to suppose that the eyes of Aeshnid larvae are more efficient in detecting prey than are those of other dragonfly larvae. This is supported by observations on the predatory behaviour of dragonfly larvae (Section 7) which show that Aeshnid larvae depend almost entirely on visual stimuli for detecting prey, whilst other forms depend to a large extent on tactile stimuli as well.



FIG. 1. - Lateral views of the heads of last instar dragonfly larvae with the labia in the resting position.

a) Sympetrum danae (Libellulidae);

b) Aeshna interrupta lineata (Aeshnidae)

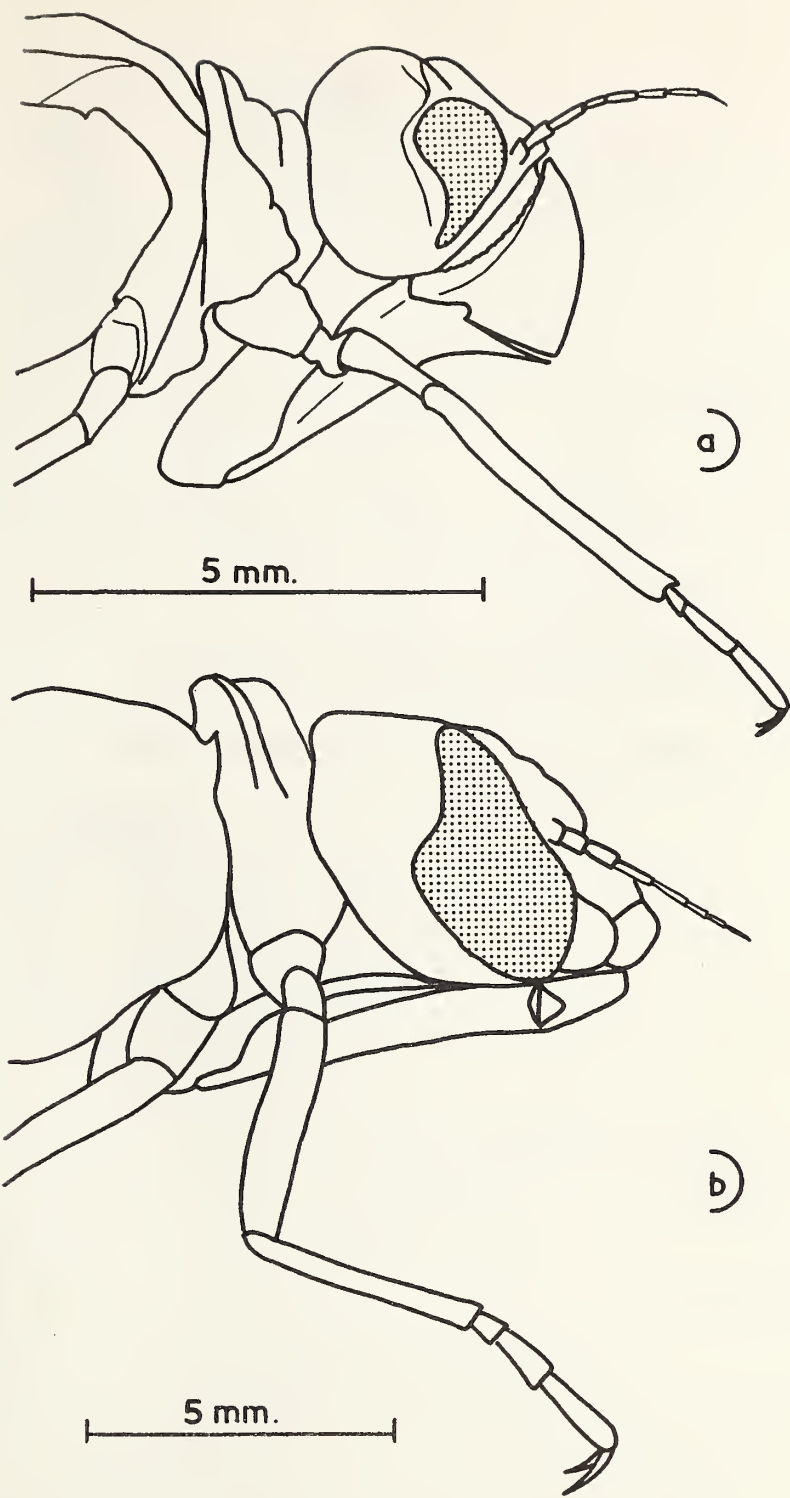


FIG. 2. - Lateral views of the heads of last instar dragonfly larvae with the labia extended.

a) Leucorrhinia borealis (Libellulidae);

b) Aeshna interrupta lineata (Aeshnidae).

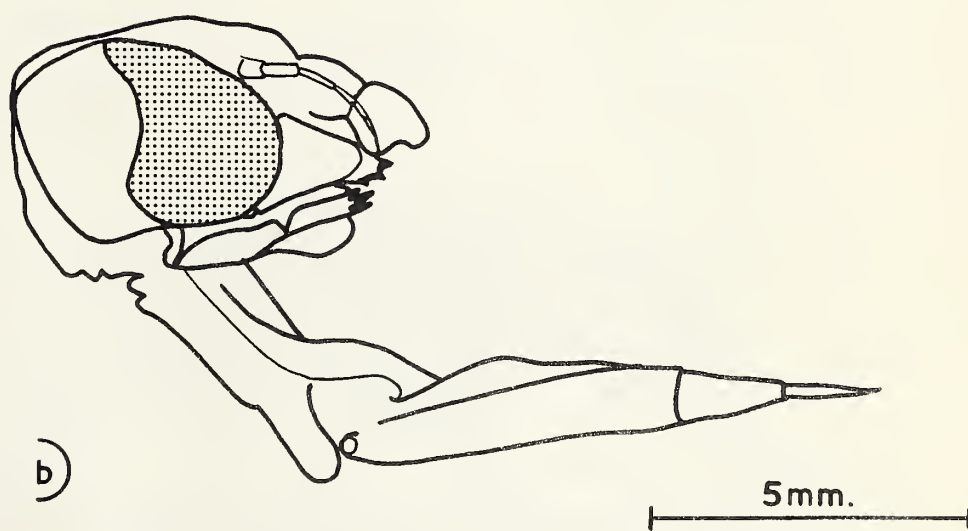
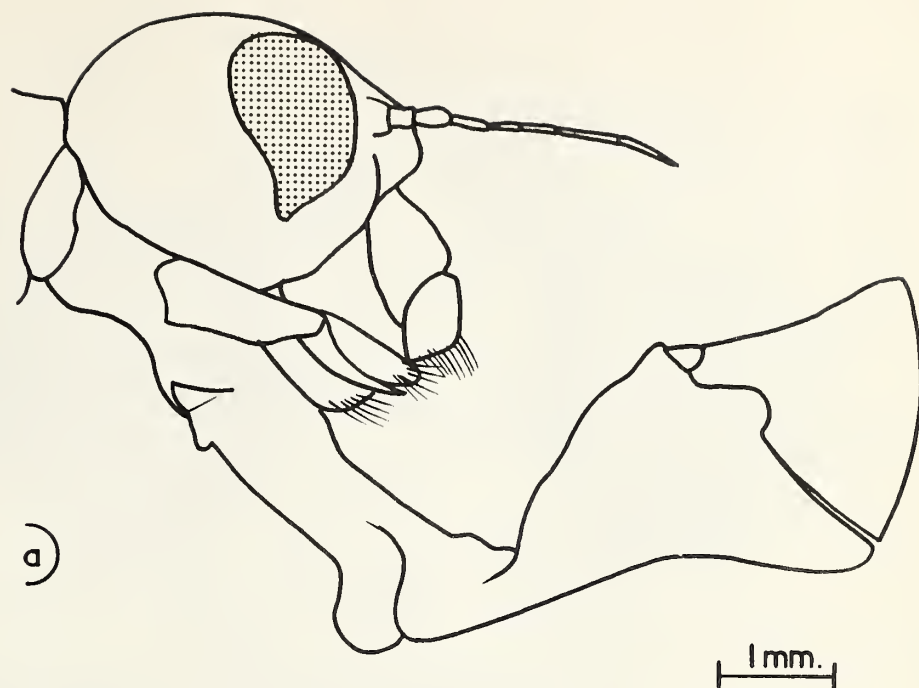
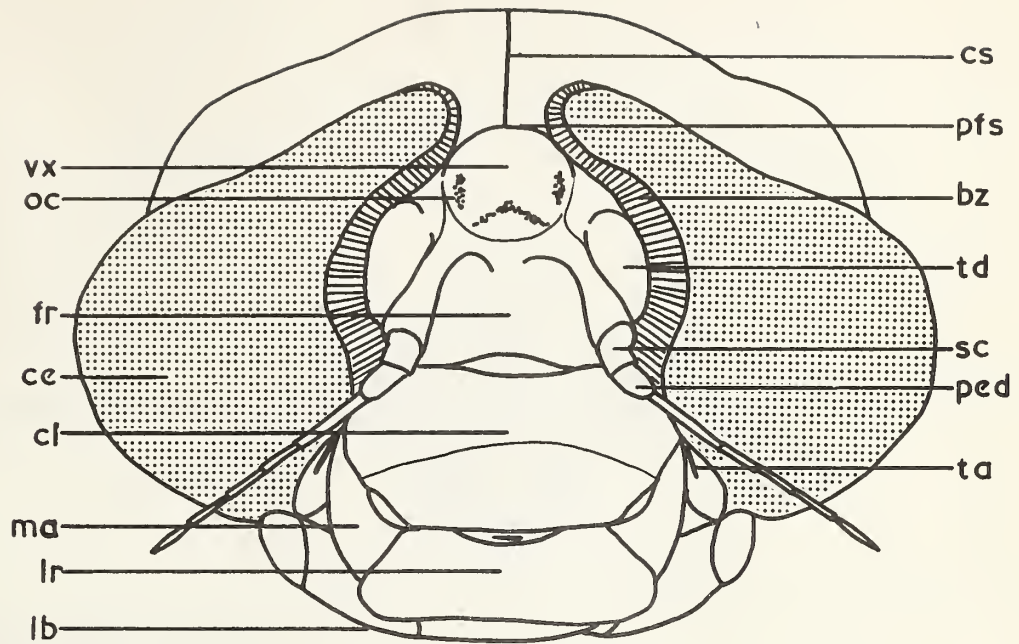


FIG. 3. - The head capsule of the larva of Aeshna interrupta
lineata.

a) Anterior view;

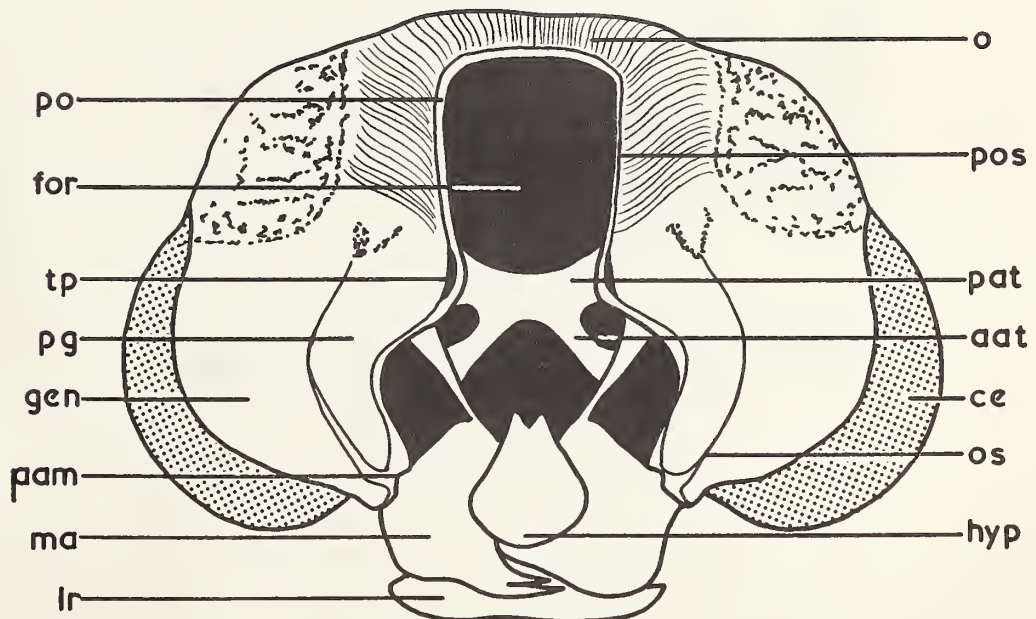
b) posterior view.

aat - anterior arm of tentorium; bz - budding zone; ce - compound eye; cl - clypeus; cs - coronal suture; for - foramen; fr - frons; gen - gena; hyp - hypopharynx; lb - labium; lr - labrum; ma - mandible; o - occiput; oc - ocellus; os - occipital suture; pam - posterior articulation of mandible; pat - posterior arm of tentorium; ped - pedicel; pfs - postfrontal suture; pg - postgena; po - post-occiput; pos - postoccipital suture; sc - scape; ta - anterior tentorial pit; td - dorsal tentorial macula; tp - posterior tentorial pit; vx - vertex.



a)

2 mm.



b)

FIG. 4. - The mouthparts of the larva of Aeshna interrupta
lineata.

- a) Anterior view of head dissected to show labral muscles;
- b) ventral view of labrum.

cplr - compressor of labrum; mlra - anterior labral
muscle; mlrp - posterior labral muscle; sens -
sensillum.

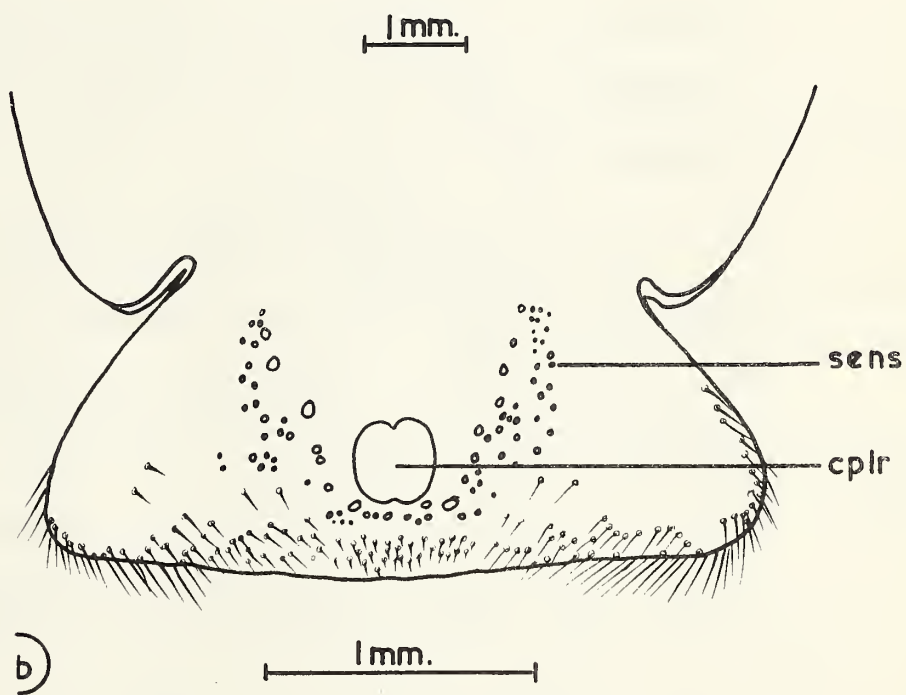
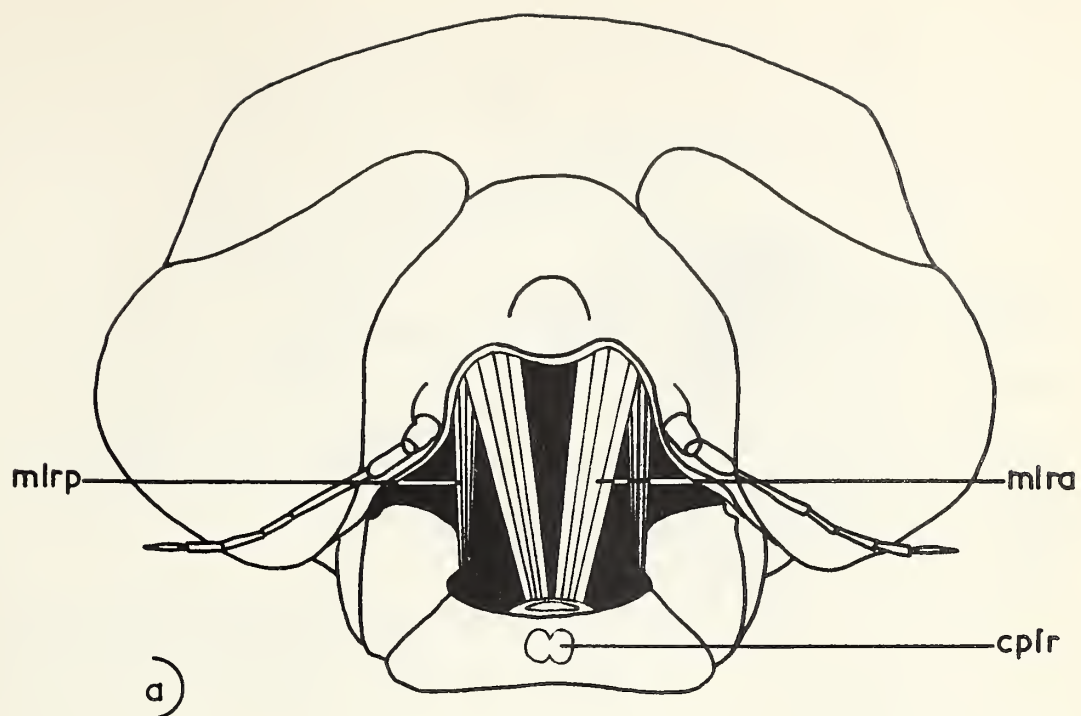
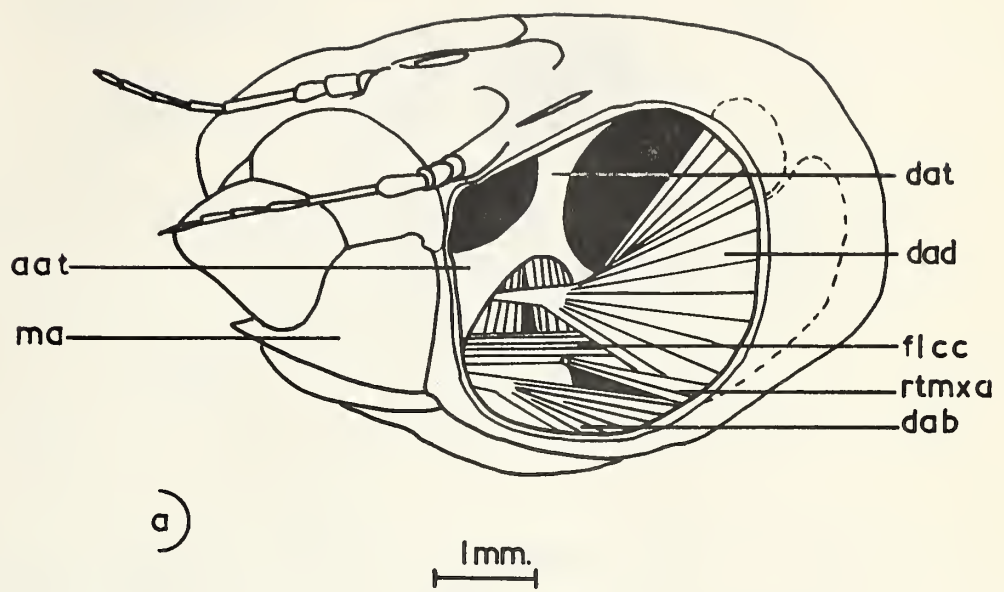


FIG. 5. - The mouthparts of the larva of Aeshna interrupta
lineata.

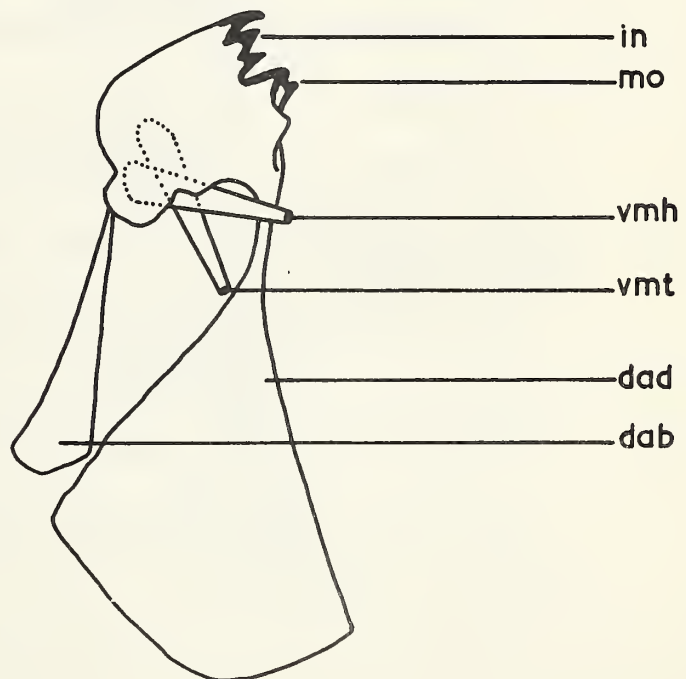
a) Lateral view of head dissected to show dorsal
mandibular muscles and some maxillary muscles;

b) anterior view of left mandible.

aat - anterior arm of tentorium; dab - dorsal abductor of
mandible; dad - dorsal adductor of mandible; dat - dorsal
arm of tentorium; flcc - cranial flexor of lacinia; in -
incisor teeth; ma - mandible; mo - molar ridge; rtmxa -
rotator of maxilla; vmh - ventral hypopharyngeal muscle of
mandible; vmt - ventral tentorial muscle of mandible.



a)



b)

FIG. 6. - The mouthparts of the larva of Aeshna interrupta
lineata.

a) Lateral view of head dissected to show maxillary
muscles;

b) anterior view of left maxilla.

adcd - adductor of cardo; adst - adductor of stipes; cd -
cardo; dpmp - depressor of maxillary palp; flcc - cranial
flexor of lacinia; flcs - stipital flexor of lacinia; lc -
lacinia; lvmp - levator of maxillary palp; mxp - maxillary
palp; rtmxa - rotator of maxilla; stp - stipes.

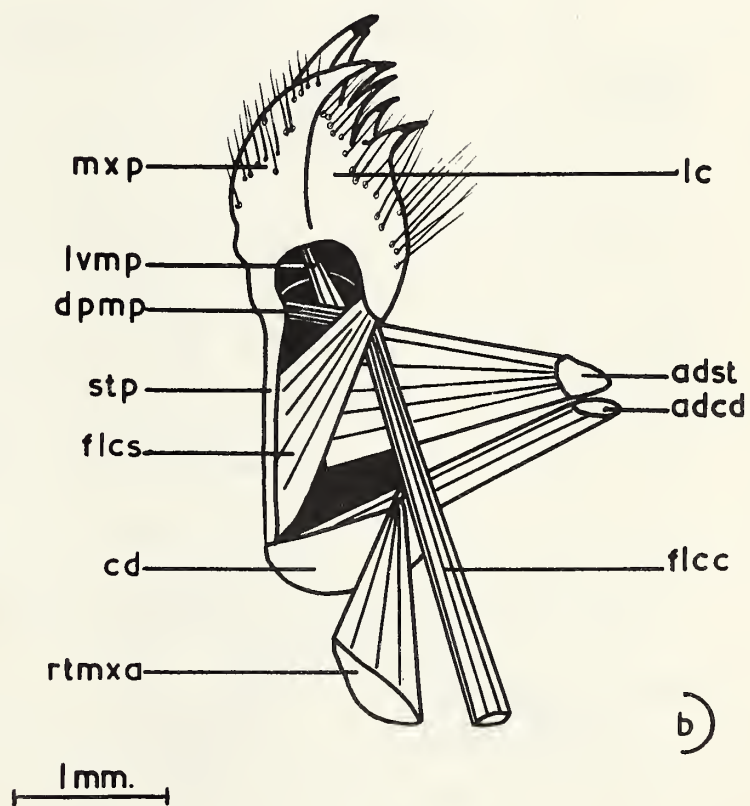
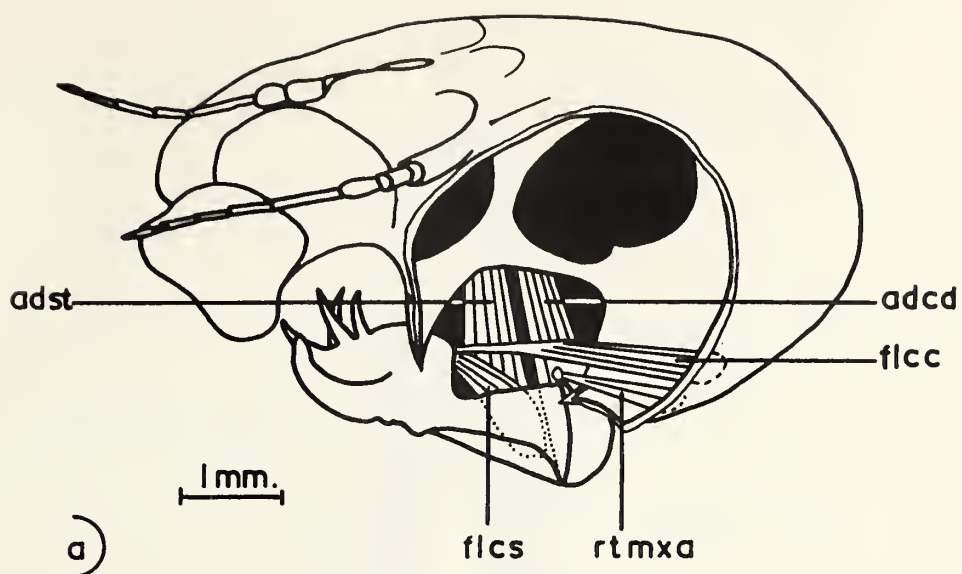


FIG. 7. - The mouthparts of the larva of Aeshna interrupta
lineata.

- a) Dorsal view of the labium dissected to show muscles;
- b) lateral view of elbow muscles of the labium.

ablp - abductor of labial palp; addlp - adductor of labial
palp; eh - end hook; exprm - extensor of prementum;
hyp - hypopharynx; lp - labial palp; mh - movable hook;
pom - postmentum; prm - prementum; rthyp - retractor
of hypopharynx; 1⁰fl, 2⁰fl, 3⁰fl - primary, secondary,
tertiary flexors of prementum.

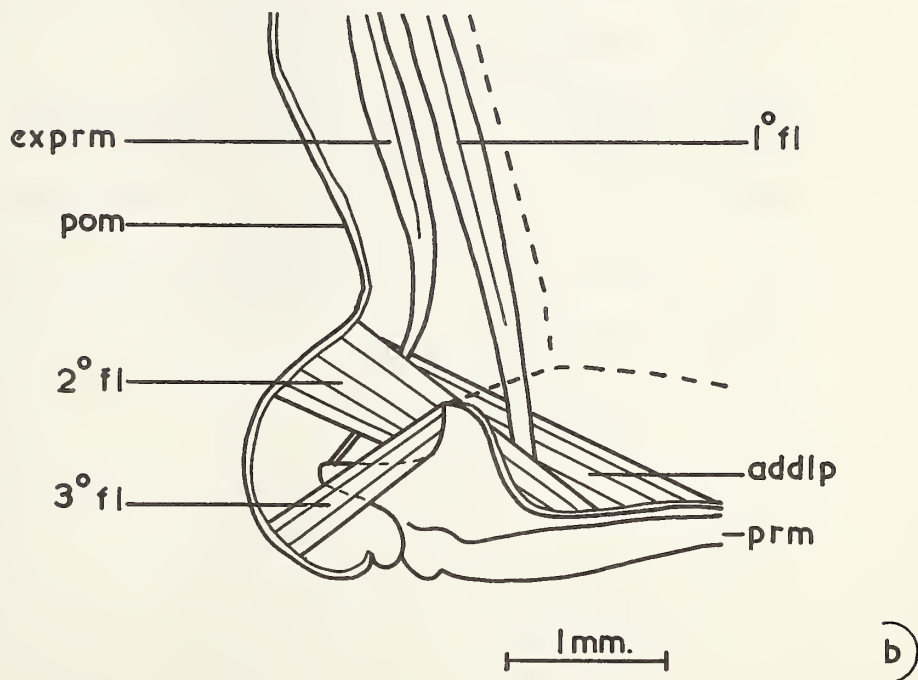
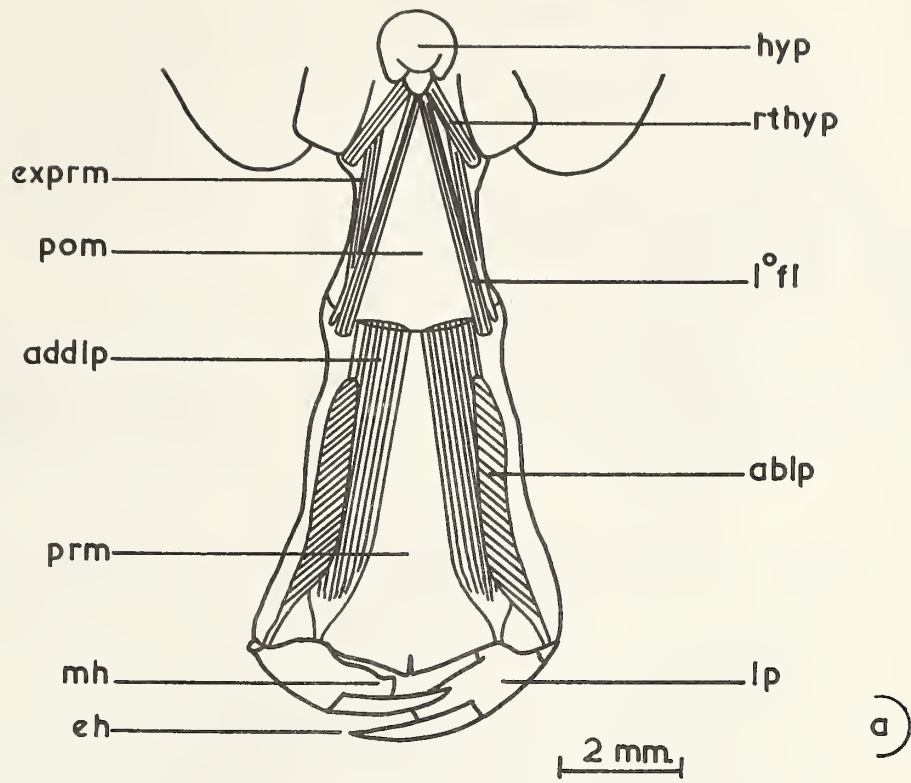


FIG. 8. - The mouthparts of the larva of Aeshna interrupta
lineata.

- a) Anterior view of hypopharynx;
- b) ventral view of hypopharynx dissected to show muscles;
- c) lateral view of hypopharynx.

exprm - extensor of prementum; hyp - hypopharynx;

rthyp - retractor of hypopharynx; sal - salivarium;

susp - suspensorium; Tap - T-shaped apodeme; vmh -

ventral hypopharyngeal muscle of mandible; 1^ofl -

primary flexor of prementum.

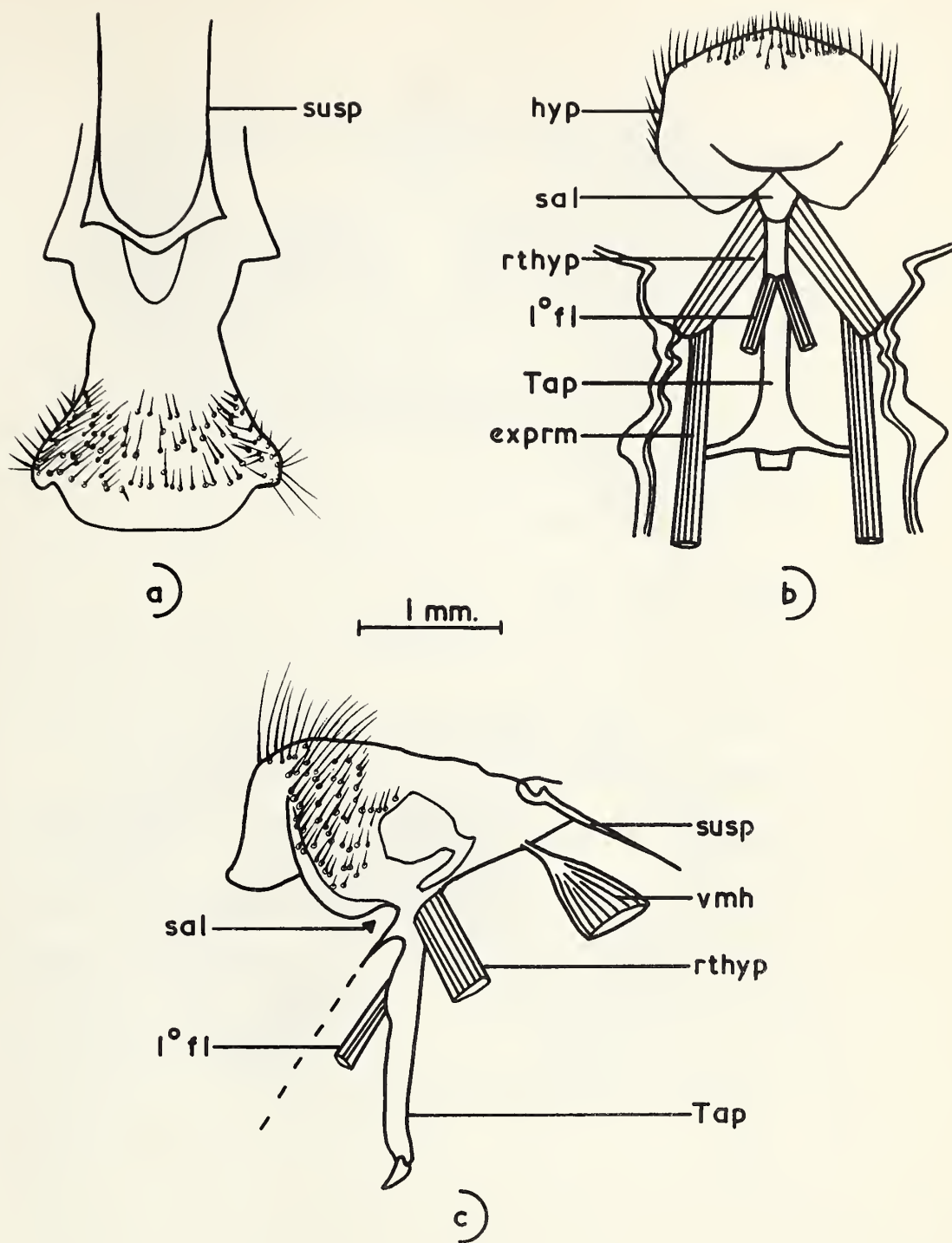


FIG. 9. - The head capsule of the larva of Libellula
quadrимaculata.

a) anterior view;

b) posterior view.

aat - anterior arm of tentorium; bz - budding zone; ce - compound eye; cl - clypeus; cs - coronal suture; for - foramen; fr - frons; gen - gena; lr - labrum; ma - mandible; o - occiput; pam - posterior articulation of mandible; pat - posterior arm of tentorium; pfs - post-frontal suture; pg - postgena; po - postocciput; pos - postoccipital suture; ta - anterior tentorial pit; tp - posterior tentorial pit; vx - vertex.

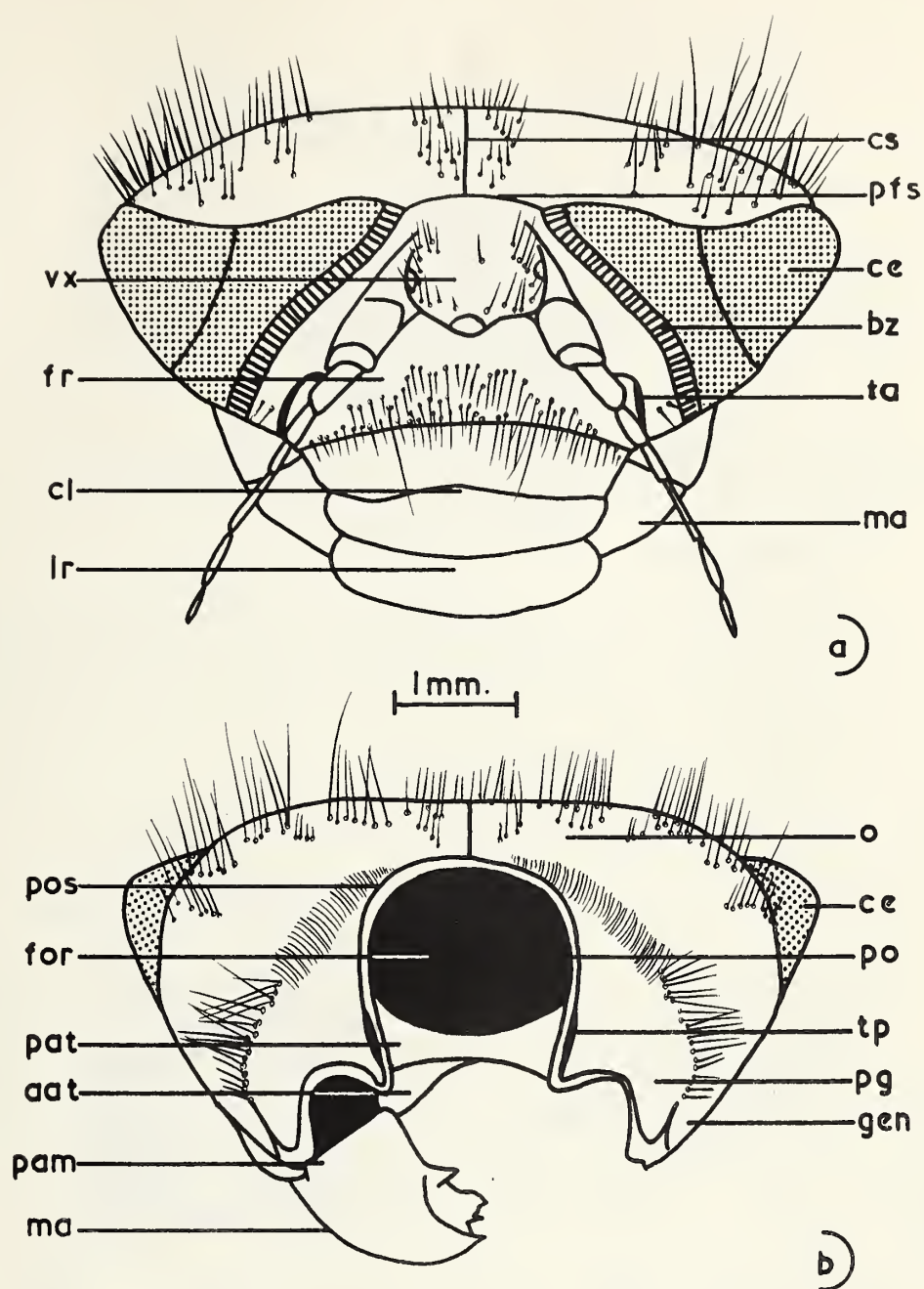


FIG. 10. - The mouthparts of the larva of Libellula
quadrimaculata.

- a) Anterior view of head dissected to show labral muscles;
- b) ventral view of hypopharynx dissected to show muscles;
- c) lateral view of hypopharynx.

cplr - compressor of labrum; exprm - extensor of
prementum; hyp - hypopharynx; lr - labrum; mlra -
anterior labral muscle; mlrp - posterior labral muscle;
rthyp - retractor of hypopharynx; susp - suspensorium;
Tap - T-shaped apodeme.

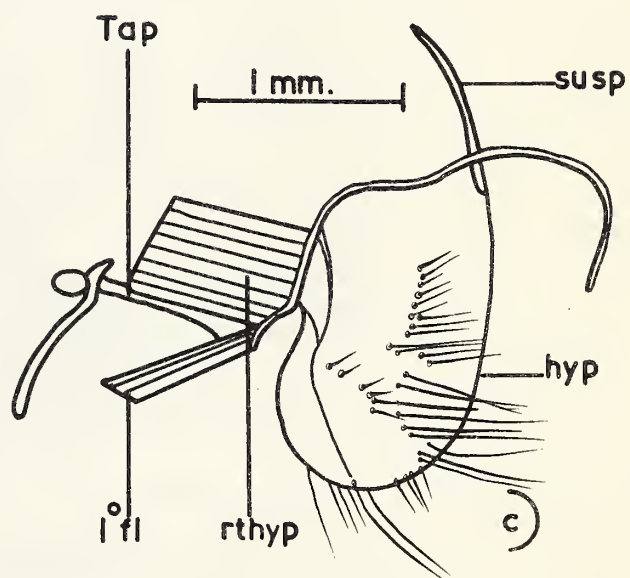
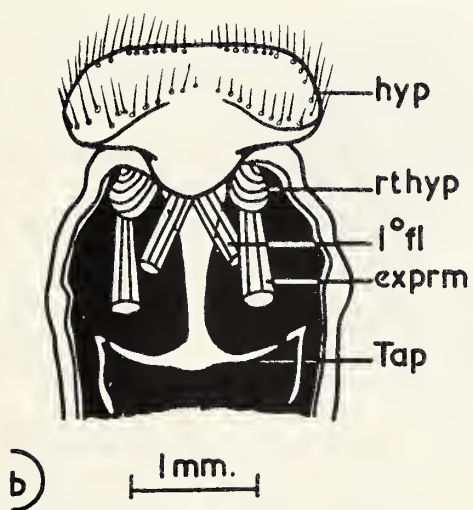
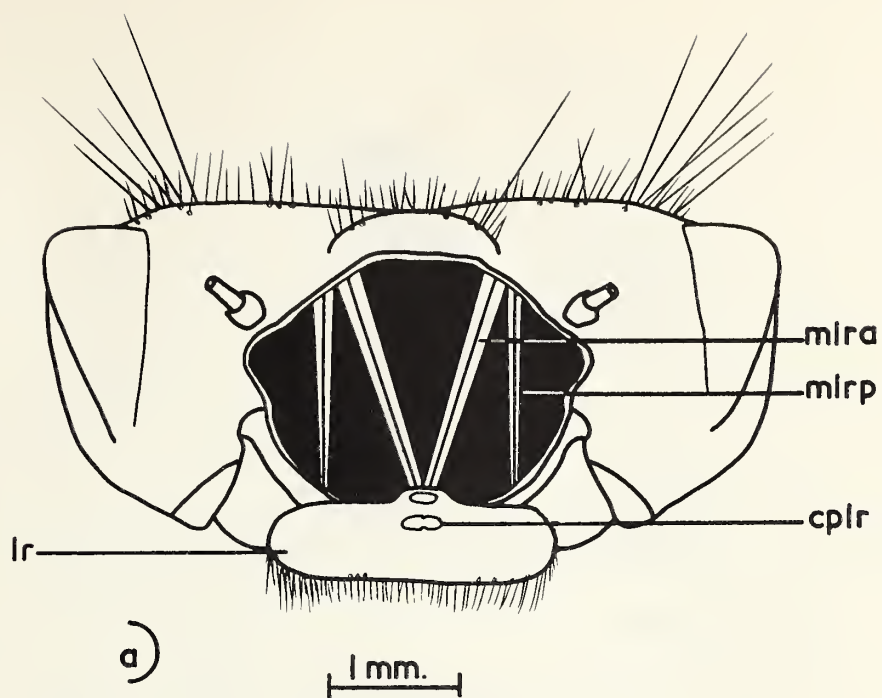


FIG. 11. - The mouthparts of the larva of Libellula
quadrimaculata.

- a) Lateral view of head dissected to show dorsal
mandibular muscles;
- b) lateral view of head dissected to show maxillary
muscles.

aat - anterior arm of tentorium; adcd - adductor of
cardo; adst - adductor of stipes; dab - dorsal abductor
of mandible; dad - dorsal adductor of mandible; dat -
dorsal arm of tentorium; flcc - cranial flexor of lacinia;
flcs - stipital flexor of lacinia; ma - mandible; max -
maxilla; rtmxa - rotator of maxilla; vmh - ventral
hypopharyngeal muscle of mandible; vmt - ventral
tentorial muscle of mandible.

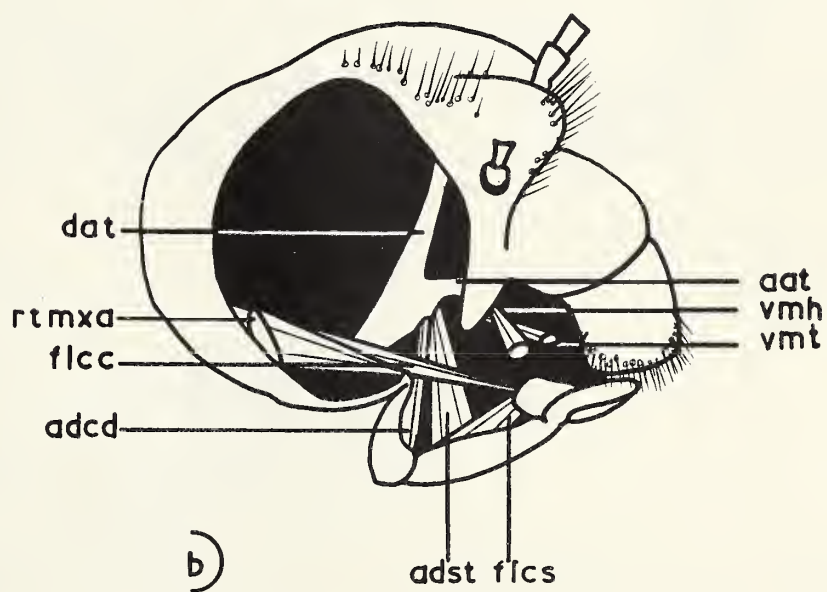
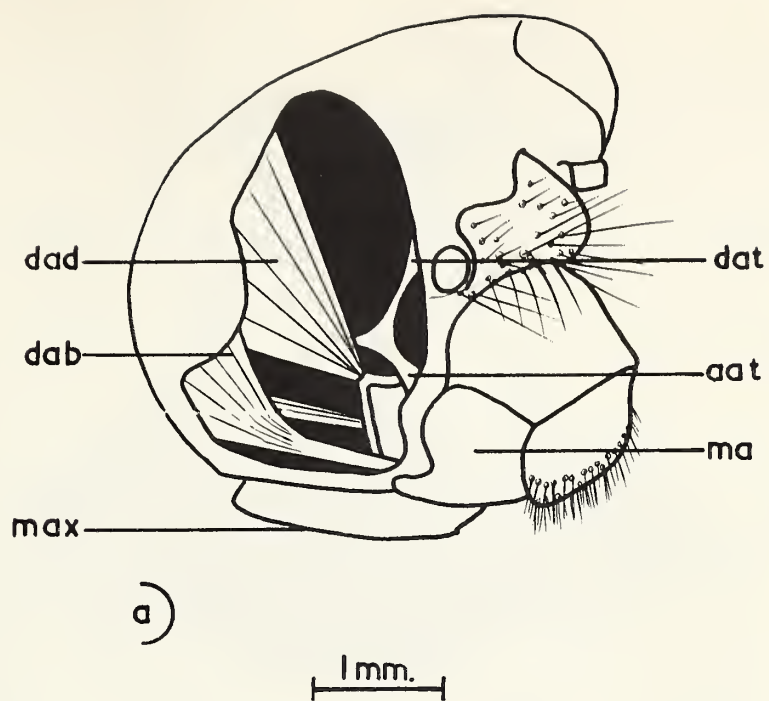


FIG. 12. - The mouthparts of the larva of Libellula
quadrimaculata.

a) Dorsal view of labium dissected to show muscles;

b) lateral view of elbow muscles of the labium.

ablp - abductor of labial palp; addlp - adductor of labial

palp; exprm - extensor of prementum; hyp - hypopharynx;

lp - labial palp; mh - movable hook; pom - postmentum;

prm - prementum; 1^ofl, 2^ofl, 3^ofl - primary, secondary,

tertiary flexors of prementum.

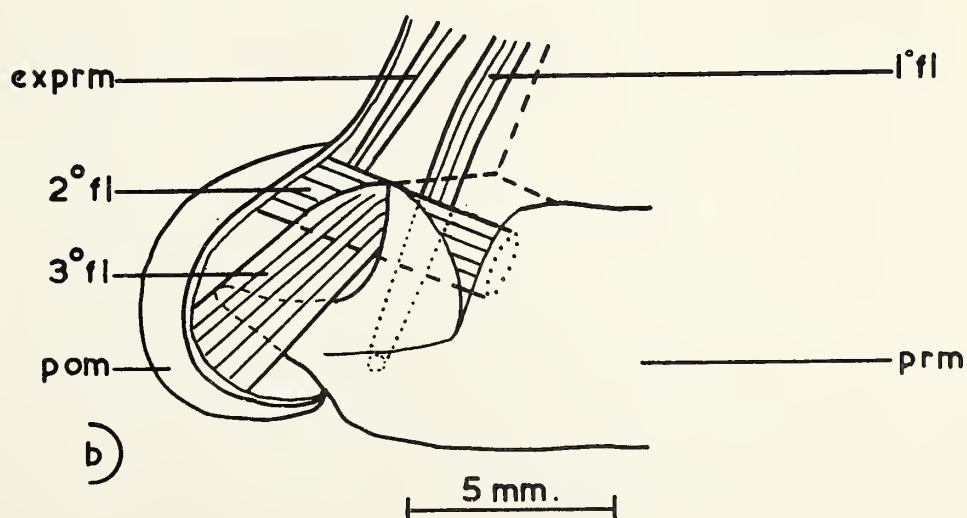
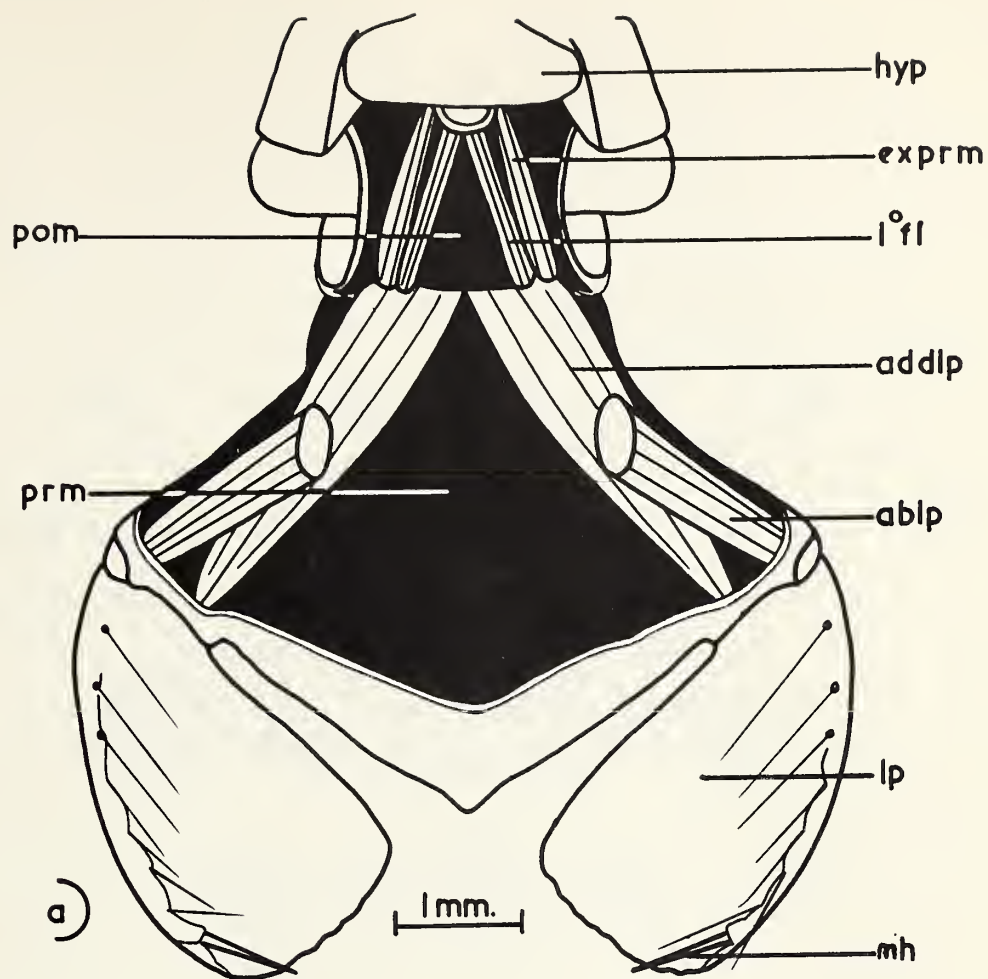


FIG. 13. - Head of Leucorrhinia intacta with labium partly
extended to show cage-like roof formed by palpal setae.

lp - labial palp; ps - palpal seta.

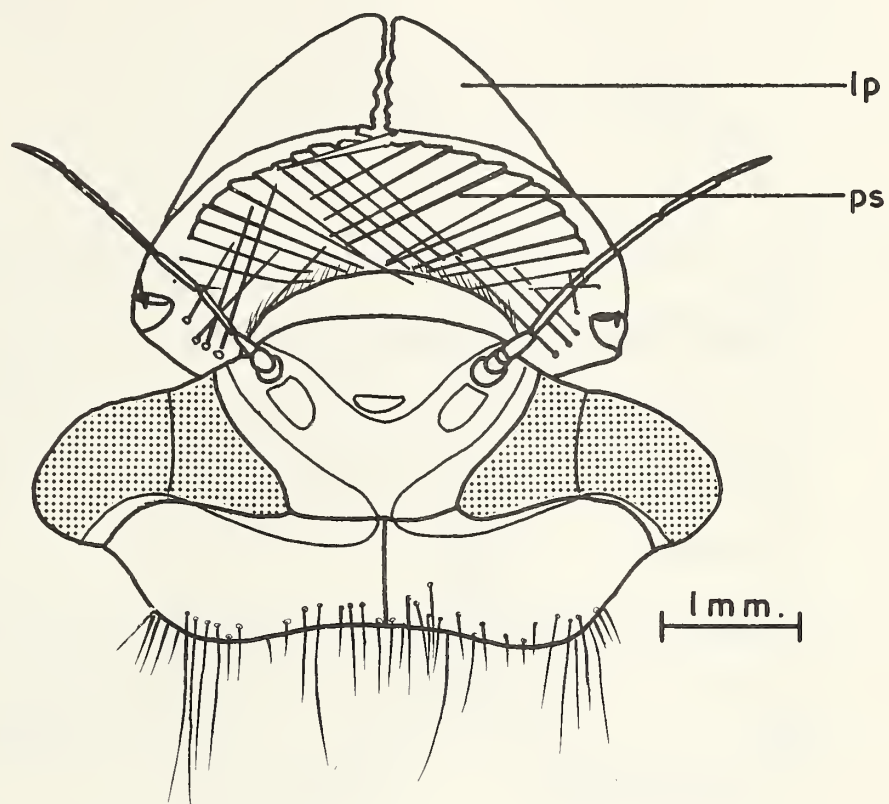


FIG. 14. - Sections through the head of the last larval instar of Aeshna interrupta lineata showing angles of vision.

- a) Transverse-vertical section; each eye covers 215° and there is an angle of binocular vision of 68° above the head;
- b) longitudinal horizontal section; each eye covers 201° and there is an angle of binocular vision of 68° in front of the head.

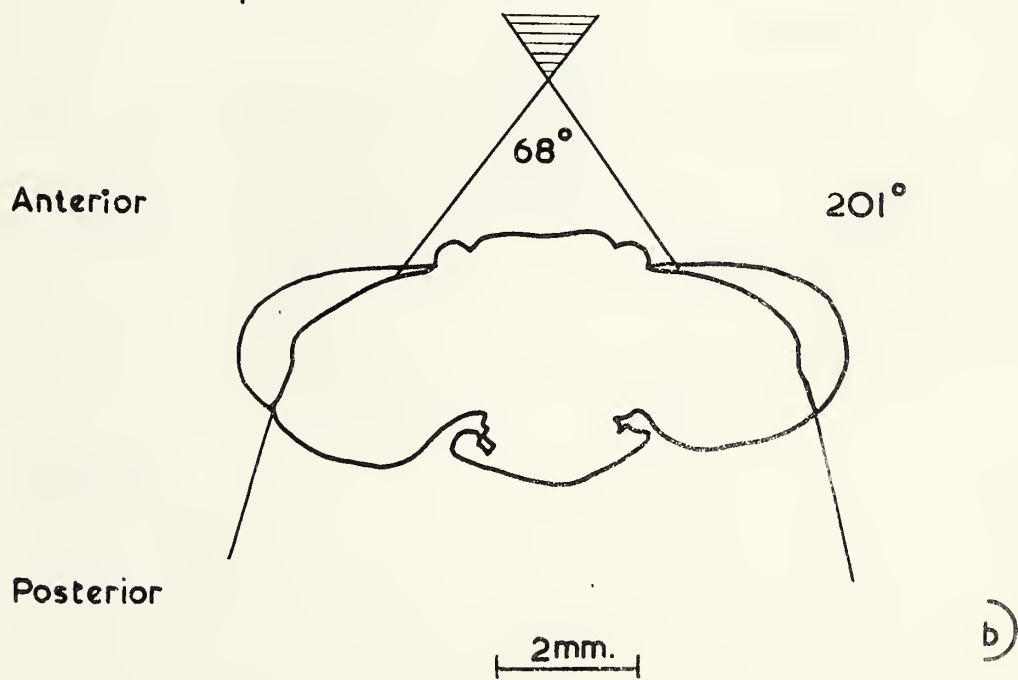
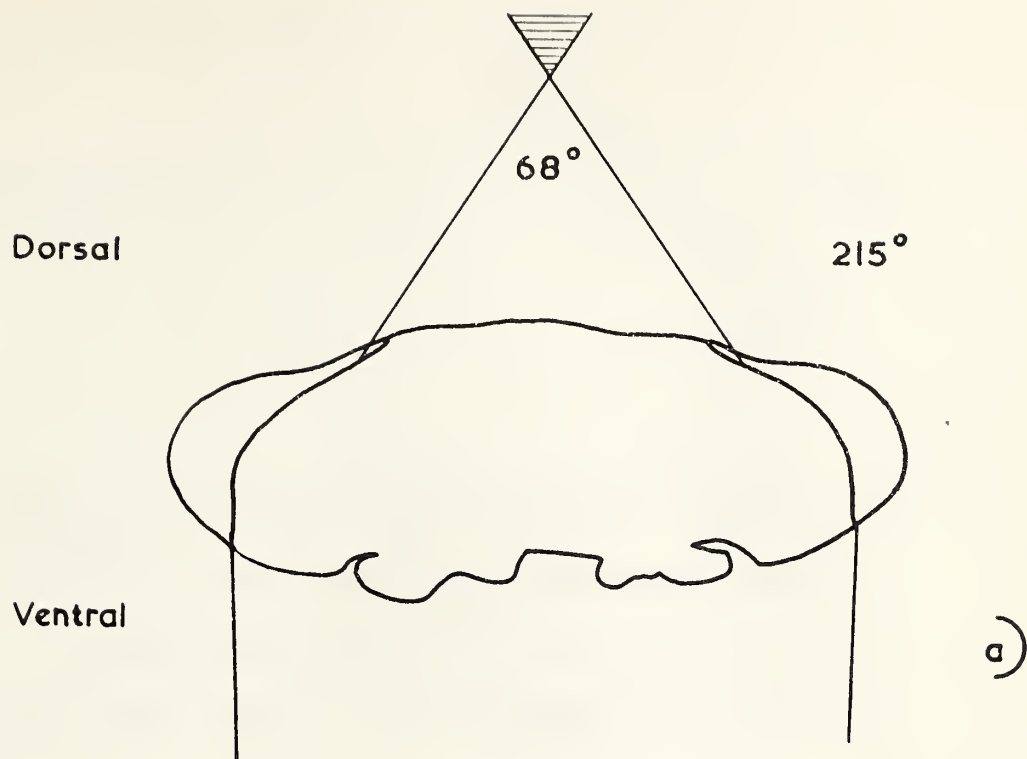
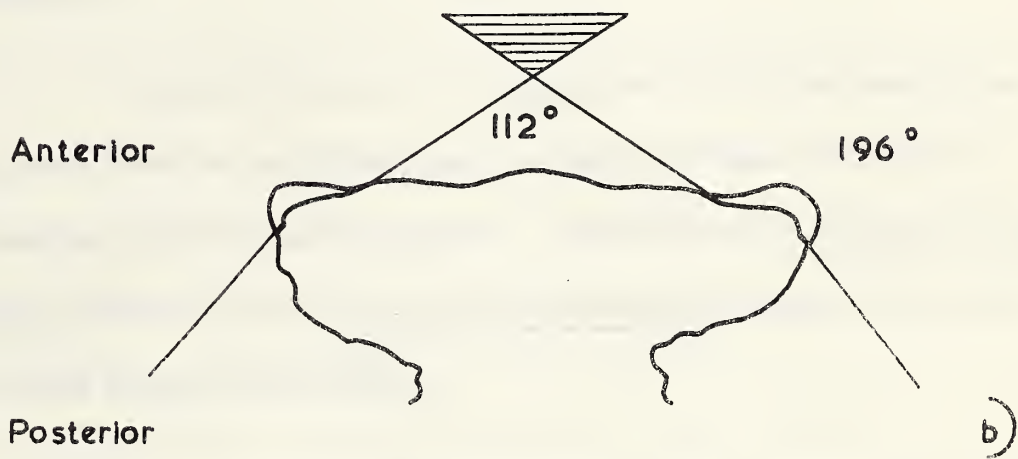
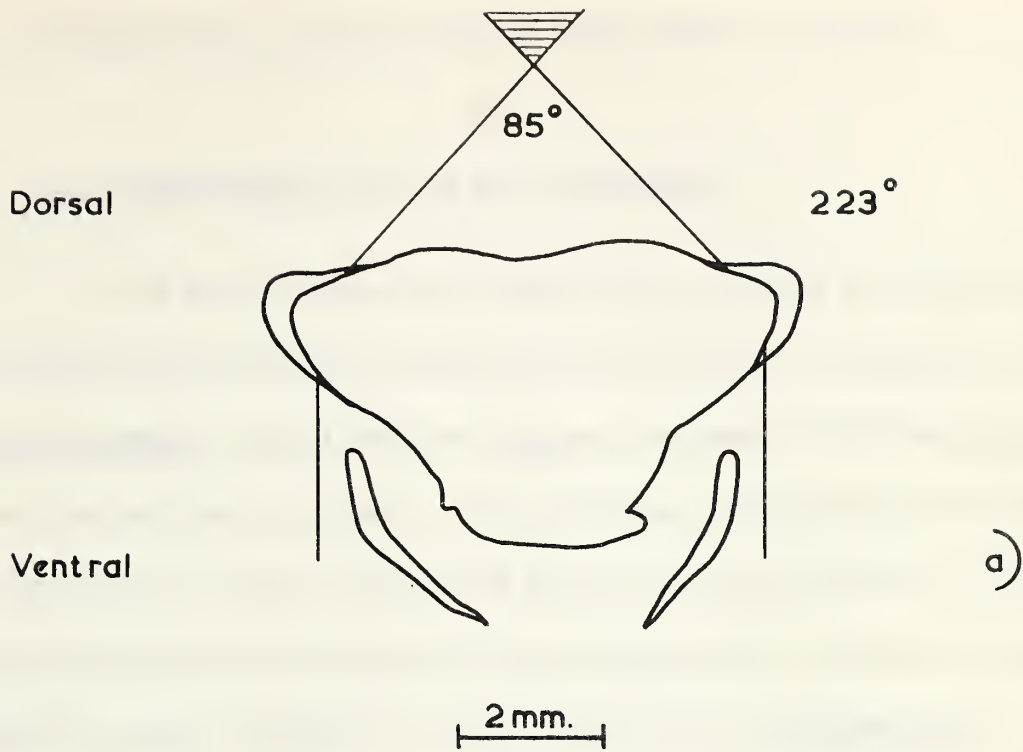


FIG. 15. - Sections through the head of the last larval instar of Libellula quadrimaculata showing angles of vision.

- a) Transverse-vertical section; each eye covers 223° and there is an angle of binocular vision of 85° above the head;
- b) longitudinal-horizontal section; each eye covers 196° and there is an angle of binocular vision of 112° in front of the head.



3. PREDATORY APPARATUS OF DRAGONFLY ADULTS

3.1 The morphology of the head and mouthparts

The head of the adult dragonfly has received a certain amount of attention from previous workers and the accounts of Chao (1953) for Onychogomphus, Short (1955) for Aeshna, and Sokal (1947) for Pantala, cover the suborder quite well. Lew (1933) has considered certain head characters of a variety of Odonates and his account includes an excellent description of the development of the compound eyes. Special mention should be made of Asahina's careful work (1954) on Epiophelebia superstes.

In view of the above work only the important head characters, including those which differ from the larva and those important in predation, will be mentioned here. The drawings of Aeshna interrupta lineata (Figure 16) and Libellula quadrimaculata (Figure 17) provide the more general information.

The principal changes that take place in the head capsule at metamorphosis are associated with the great development of the compound eyes. The eyes of all adult dragonflies are large but especially so in the Aeshnidae and the Libelluloidea, in which they are confluent for some distance on the top of the head and the coronal suture is here invaginated. The eyes also extend ventrally and the

genae are almost completely lost; remnants occur below and behind the eye, although in this latter region the gena cannot be distinguished from the postgena for the most part because of the obscure nature of the occipital suture. In contrast with the larvae, adult dragonflies use only sight in the detection of prey and the antennae are much reduced.

The frons (fr) of the adult is usually large and bulging, this protuberant nature being best developed in Libelluloids where it is perhaps associated with the somewhat inflated condition of the larval frons above the labial mask. The adult clypeus is divided into a large postclypeus (pclp), which continues the line of the frons, and a smaller, slightly recessed anteclypeus (aclp). The frontoclypeal suture is well defined and is invaginated as the strengthening epistomal ridge internally. The vertex (vx), or the area between the ocelli (vertical or frontal tubercle of Asahina, 1954), is also well developed in many species. It bulges out considerably in Libelluloids and forms a ridge between the two lateral ocelli in Aeshna, but in Gomphids, where the three ocelli lie in a single line, it is not protuberant. These inflated areas on the head of adult dragonflies contain air sacs.

The eyes extend only slightly over the posterior surface of the head, which is composed mainly of occiput (o). This region is deeply concave and overlaps the prothorax, so allowing proprioceptive hairs to give information concerning the relative positions of the head

and thorax during flight (Mittelstaedt, 1950).

The mouthparts of adult dragonflies are adapted for holding and chewing prey whilst in flight. As in the larva, it is the labium that is most modified to this end, whilst the labrum, mandibles, and hypopharynx show slight but constant differences from the larval state. Only the maxilla passes through metamorphosis unaltered.

The labrum (Figures 18 and 19a) is subrectangular in shape and attached proximally to the anteclypeus. On the adoral side, the epipharynx is a raised central area bearing sensilla (sens) and it is bordered laterally by short, stiff setae which point mesally. The sensilla, which are described in Section 4, appear to have a gustatory function. Just behind the area of sensilla is a pair of brushes (br) which point orally. Each brush is composed of a number of spines borne on a short protuberance, and it is presumed that they are concerned with the direction of food towards the mouth. Such brushes have not been found in larvae. In the adults of certain species, short spines are found posterior to the brushes, but they appear to be absent in Libelluloids.

The anterior (mlra) and posterior (mlrp) labral muscles originate together on the frons and are inserted medially on the dorsal side of the labral base and on the tormae respectively. The labral compressors run from the dorsal to the ventral walls of the labrum.

The mandibles are stout, heavily sclerotized structures whose distal ends are divided into a number of strong teeth, the arrangement of which differs slightly from that in the larva. The number of incisor teeth is reduced to three and the molar area is transposed from a single ridge to a Z-shaped ridge set on a broad base. The articulations and the musculature are basically the same as in the larva.

The hypopharynx differs from that of the larva in that the T-shaped apodeme is absent; a small flap at the base of the hypopharynx may represent a vestige of its former elongated structure. The primary flexors of the prementum now originate alongside the retractors of the hypopharynx on a strengthening bar which runs around the lateral walls of the hypopharynx to the salivarium.

The labium of adult dragonflies (Figures 19b, 20, 21 and 22) is cuplike, formed of broad sclerites which can effectively enclose the other mouthparts. The postmentum (pom) is rectangular in shape and its two proximal angles articulate with the hypostoma of the head capsule. The retractor muscles of the hypopharynx (rthyp) are attached to ridges on the postmentum just before the articulations. The ventral side of the postmentum is well sclerotized and strengthened by ridges which serve for muscle attachments, but the dorsal side is membranous and flexible. The prementum (prm) is similarly sclerotized ventrally and is more membranous dorsally, and it supports the median lobe (ml)

or ligula anteriorly, and the palpigers (pag) laterally. The lateral lobes (lp), which represent the first segment of each labial palp, are broad, flat sclerites which move on the palpigers.

The relative sizes and shapes of these labial sclerites vary within the Anisoptera. In Gomphids and Aeshnids (Figure 20), the lateral lobes, although large, do not meet in the mid-line and the median lobe is large and visible from the dorsal side. Each lateral lobe in these groups bears a sharp end hook (eh) at the inner distal angle and a blunt movable hook (mh) which represents the second segment of the labial palp. In some Aeshnids (e.g. Aeshna spp.) there is a small cleft in the median lobe and on each side of this cleft are small sclerotized points. In Aeshna, the sclerotized points and the end hooks project upwards into the preoral food cavity and serve to hold food that is being chewed.

In Cordulegaster boltonii (Donovan) (Figure 21), the lobes are the same relative sizes as in Aeshna, but the median lobe is broadly cleft to one-fifth of its length and each lateral lobe bears a series of teeth on its inner edge. The outer tooth of the lateral lobe is large and points towards the mouth as does the end-hook of Aeshna, and the other teeth lie inwards from this and have no strict pattern, even between the lateral lobes of a single labium. This dentate condition is present also in the larva of Cordulegaster.

In Libelluloids, the lateral lobes are large with straight inner borders that meet in the mid-line and so cover the median lobe from the dorsal aspect. The balance between archaic and recent characters in the wing venation has been used as a basis for the classification of the Libellulidae by Fraser (1957) and it is interesting to note that, in the species studied here, the size of the lateral lobes relative to the other sclerites increases as the number of recent venational characters increases (Figure 22). The movable hook is absent from Libelluloid labia and the end hook is reduced.

There are only four pairs of true labial muscles in the adult dragonfly (Figure 19b). Whedon (1927) described five pairs in Anax junius but his description of a pair of large extensor muscles has not been confirmed ^{by} other workers. The adductors of the lateral lobes (addlp) originate medially at the distal end of the postmentum and they insert mesad of the articulations of the lateral lobes with the palpigers. The primary flexors of the prementum (1^{ofl}) are inserted at the proximal end of the prementum and they originate on the basal strengthening bar of the hypopharynx. The secondary (2^{ofl}) and tertiary (3^{ofl}) flexors are small muscles which pass from the postmentum over the hinge line to insert on the palpigers. These flexor muscles acting on the prementum and indirectly on the lateral lobes through the palpigers, serve to increase the cup-like nature of the labium, enclosing the other mouthparts and preventing the escape of prey.

The two pairs of muscles that are not carried over from the larva to the adult are the extensor of the prementum and the abductor of the palp, both of which are important in prey capture by the larva. The labium of the adult is not extensible and an extensor of the prementum would serve little useful purpose, whilst a rapid opening of the palps is not necessary and the elastic nature of the cuticle is sufficient to produce the required outward movements of the labial palps.

The retractors of the hypopharynx are also attached on the labium and Short (1955) believes that they serve to produce some extension of the adult labium, and suggests that this is the reason for their shift in origin from the larval condition. But these muscles are inserted so close to the articulation of the postmentum with the head that any action they may have on the labium would be most inefficient. Short believed that this muscle presented itself as a substitute extensor of the labium in place of the larval extensor which is lost at metamorphosis, but he was confused over the function of the latter muscle, having assumed that it extended the postmentum. He missed the lever-like extensions of the prementum on which this muscle actually inserts in the larva, and apparently did not notice the anterior point of articulation of the larval postmentum. It is suggested here that the retractors of the hypopharynx produce little or no movement of the labium.

3.2 The morphology of the eyes

Adult dragonflies detect and orientate towards prey exclusively through the use of visual stimuli. Good vision is essential and it is not surprising that dragonflies have the largest eyes of all insects. Hooke (1665) was impressed by the number of ommatidia, and Tillyard (1917) gives this number in each eye as between 10,000 and 28,000, the former figure for Zygoptera and the latter for large Aeshnines. I have counted about 22,650 facets in each eye of Aeshna interrupta lineata, and the smaller Libellulid Sympetrum danae has about 10,950 per eye. Both of these counts were for males but it seems unlikely that the female would differ significantly, since the main features of the eye are associated with prey capture which is conducted in the same manner by both sexes.

A wide field of view is important in the detection of prey, for the greater the area covered by the eyes the greater will be the amount of available food. The eyes of all dragonflies that have been studied are capable of covering the full 360° of the transverse-vertical plane without the head being moved. In both Aeshna eremita (Figure 23a) and A. interrupta lineata, each eye covers a field of 208° in this plane, there being overlaps of the two visual fields dorsally and ventrally. These areas of binocular vision vary in different parts of the eye, but above the head 22° of the visual field is covered by both eyes, whilst the overlap below the head reaches a maximum of 34° in

the antero-ventral region. Each eye of Libellula quadrimaculata (Figure 24) covers about 198° in the transverse-vertical plane and, of this, 20° above the head is covered by the other eye also. In the species so far considered the eyes are confluent on top of the head, but in some this is not the case. The eyes of Ophiogomphus colubrinus Selys (Figure 24c) do not meet, but even so the 360° of the vertical plane are covered adequately, with an angle of binocular vision of 14° above the head. Directly below the head the overlap of visual fields is small (6°) but this increases in the antero-ventral parts of the eyes.

The field covered by the eyes in the horizontal plane is generally less than the vertical coverage. Directly in front of the head of A. eremita is an angle of 22° which is covered by both eyes and, in addition to this, each eye covers 180° by itself (Figure 23b). It is possible that Aeshna may also have an overlap of the two visual fields behind the head. The eyes of L. quadrimaculata cover a field of view of 340° in the horizontal plane, 20° of which is seen by both eyes (Figure 24b).

Adult dragonflies thus have a good visual command of their immediate environment and it is doubtful whether Δ the large eyes, assisted by a very mobile head, miss sight of any potential prey that comes within range. Binocular vision aids in the perception of distance and in orientation towards the prey, and its disposition above, in front,

and especially in the antero-ventral region of the head aids in the manoeuvres whereby dragonflies, which have detected prey above them, align themselves so that the prey is caught by the legs.

The visual acuity of the insect eye depends in part on the dimensions of the ommatidia and in part on the distribution of pigment. In general, the smaller the inter-ommatidial angle the greater is the visual acuity, and this character varies in different parts of the eye of an adult dragonfly. The diameters of the individual facets are greatest in the upper part of the eye, there is a fairly sharp transition at about the middle of the eye, and the smallest ommatidia are distributed antero-ventrally. The sizes of the ommatidial angles follow the distribution of facet diameters, although the correlation is not perfect for the almost flat upper surface of the eye and its depth in this region produce a comparatively smaller ommatidial angle than would be expected from the diameters. The inter-ommatidial angle in the upper regions is, however, about 1° as compared with angles as low as $24'$ in the antero-ventral part of the eye of Libellula quadrimaculata. The mean ommatidial angle in the vertical plane is $51'$ for Aeshna eremita and $57'$ for Libellula quadrimaculata. Ophiogomphus colubrinus has fewer ommatidia and the mean ommatidial angle is somewhat larger at $1^{\circ}6'$. The eyes of adult dragonflies are slightly astigmatic, the facet diameters and ommatidial angles being generally larger in the horizontal plane than

in the vertical.

A decrease in facet size towards the ventral side is fairly general in flying insects and may be associated with the dorsal light reflex and with an optomotor reaction. The condition is well marked in male Tabanids (Hooke, 1665), male Bibionids and male Simuliids (Imms, 1957), and in many insects with divided eyes, such as Gyrinids and male Baetids. In the last group, the large facets of the dorsal part of the eye are directed upwards and are thought to be an aid to detecting the female during the nuptial flight (Spiehe, 1940).

Dragonflies which remain immobile on perches and wait for prey, always rest with the large dorsal ommatidia directed upwards or towards the area in which prey will appear. In these forms, the large ommatidia are completely unpigmented (Figure 24) and thus function superpositionally, whilst the lateral and lower ommatidia are well pigmented and form apposition images. It is not known whether the ommatidia of these two regions differ in their basic construction, but the distribution of pigment is probably as important in governing the perception of form of the prey as is the variation in ommatidial angles. In the upper, unpigmented ommatidia, visual acuity has been sacrificed for increased luminosity of the image and hence more efficient initial detection of prey. Such a markedly discontinuous pigment distribution is characteristic of Libellulids and Gomphids and of Cordulia shurtleffi, which often catches prey from a

perch, although it can also remain airborne for long periods. Aeshnids, which never fly at prey from a perch and must detect prey at all angles to the head, have an even distribution of pigment throughout the eye.

It appears that the part of the dragonfly eye that will best form clear images is the antero-ventral region, in the area of greatest binocular coverage. Prospective prey will usually be detected by the large ommatidia and then, as the dragonfly orientates correctly towards its prey, so the form of the latter will be seen more and more clearly as it is approached.

3.3 The thorax and legs

The skewness of the thorax in the Odonata has received much attention in the past (see Needham and Anthony, 1903) and need not be considered in detail here. In short, an upgrowth of the mesepisterna and a downgrowth of the metepimera are associated with a backward displacement of the wings and a forward position of the legs. St. Quentin (1953) believes that a strong development of the wing muscles led to the forward displacement of the legs, bringing them into a position where they were available for food collection. On the other hand, it may be argued that selection acted primarily on the use of the legs for prey capture and that the backward movement of the wings was secondary to this. The lengthening of the abdomen and the manner by which head-heaviness is counteracted, are discussed by Strickland (1946).

The position and construction of the legs in modern Odonata renders them useless for walking and, on land, they are generally used only for perching. Neville (1960), however, noted that Tetrathemis camerunensis Karsch in Ghana would crawl about three inches before taking off. But the main modifications of the legs are associated with their use as organs of prey capture. The tibiae and tarsi of all legs bear long, sharp spines which overlap to form a cage-like structure when the legs are brought together. On each tibia there are two rows of spines, those of the inner row pointing medially and those of the outer row directed anteriorly. On the tibia of the fore leg the spines of the inner row are longer but fewer than the anteriorly directed spines, and a distal series of the latter are flattened and are perhaps used for eye cleaning (St. Quentin, 1936). On the middle and hind legs the spines of the two rows are more nearly of equal lengths. There are two rows of spines on the tarsi also, and each femur bears a series of very short spines.

The hind legs are somewhat longer than the middle legs and much longer than the fore legs, and this condition is important in both prey capture and in perching. The use of the legs is discussed in Section 8.1.

In considering the morphological adaptations for feeding we should not forget the exceptional powers of flight which enable dragonflies to manoeuvre well in the air and catch elusive flying prey.

FIG. 16. - The head capsule of the adult of Aeshna interrupta
lineata.

a) Anterior view;

b) posterior view.

aclp - anteclypeus; cd - cardo; ce - compound eye; fr -
frons; lb - labium; lr - labrum; o - occiput; oc - ocellus;
pclp - postclypeus; po - postocciput; vx - vertex; tp -
posterior tentorial pit.

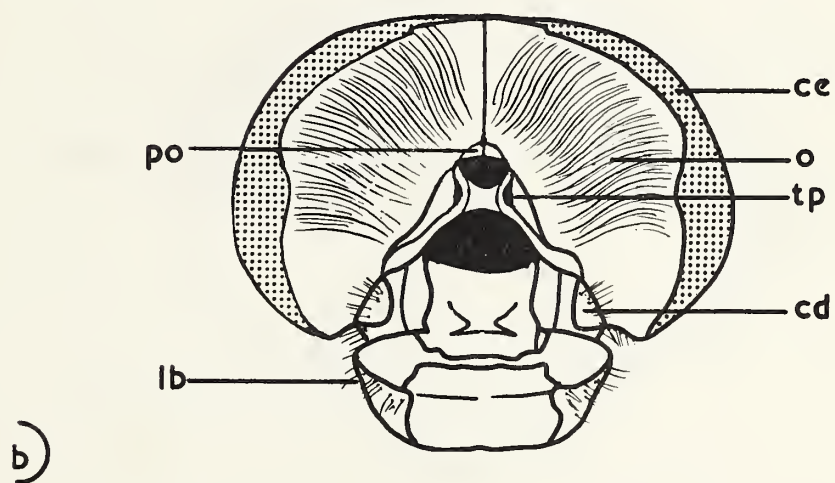
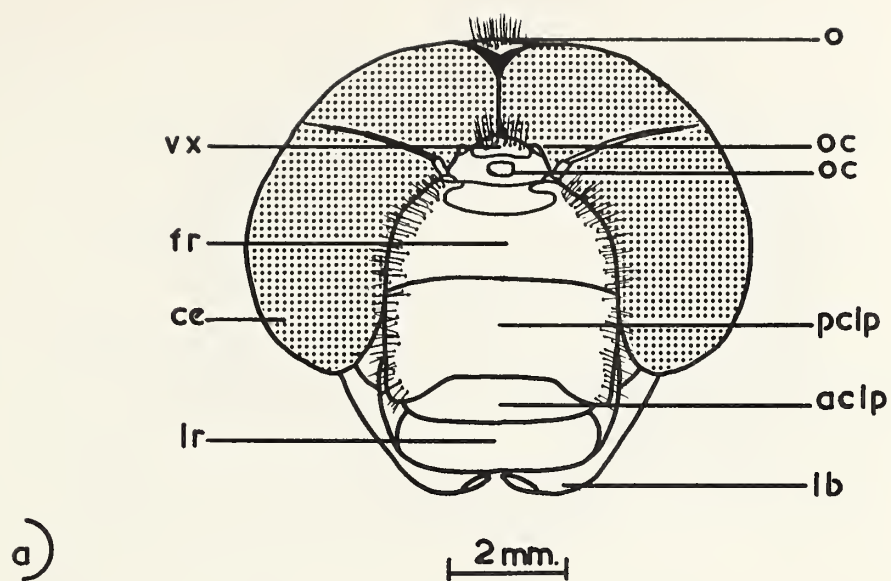


FIG. 17. - The head capsule of the adult of Libellula
quadrимaculata.

a) Anterior view;

b) posterior view.

aclp - anteclypeus; ce - compound eye; fr - frons;

lb - labium; lr - labrum; ma - mandible; o - occiput;

oc - ocellus; pclp - postclypeus; po - postocciput;

pos - postoccipital suture; tp - posterior tentorial pit;

vx - vertex.

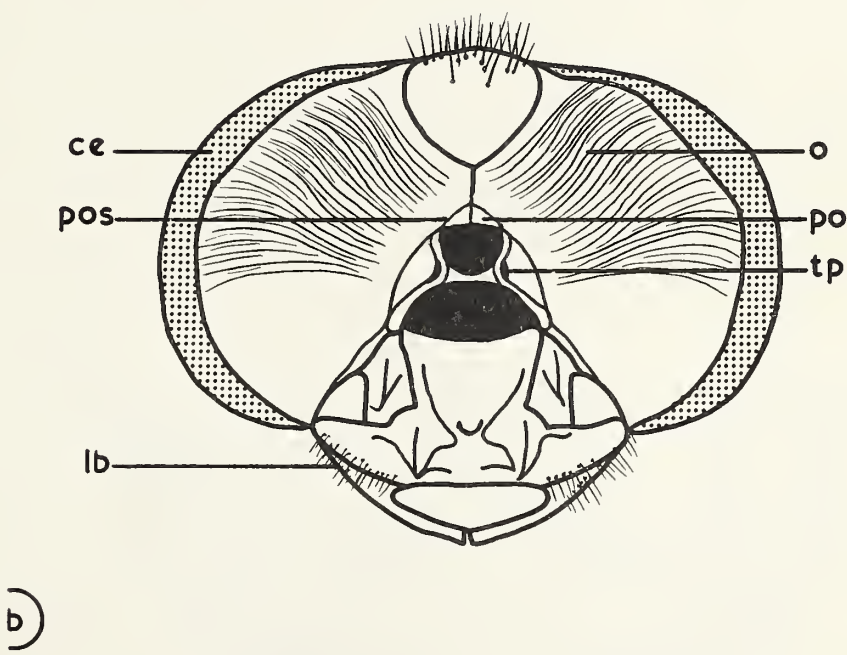
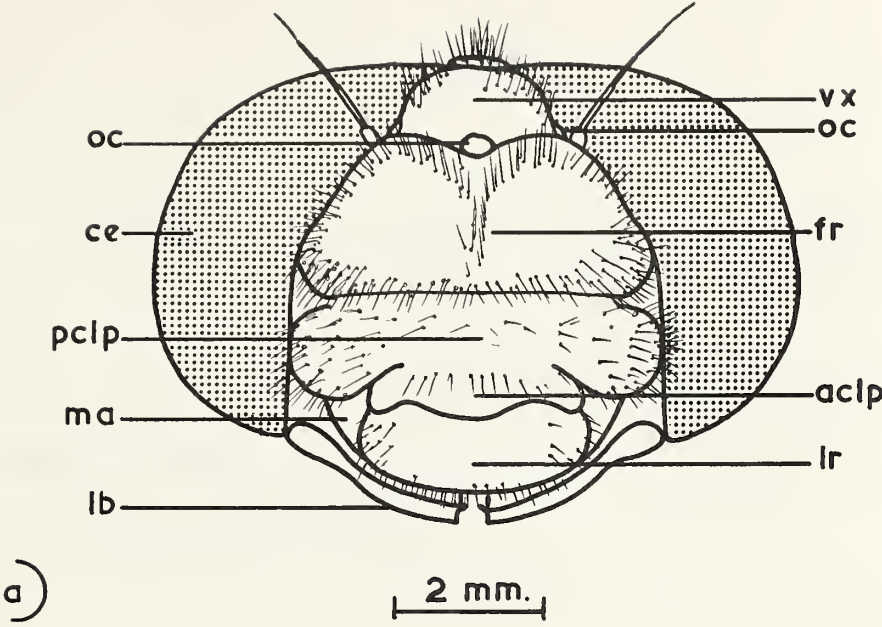


FIG. 18. - The mouthparts of adult dragonflies.

a) Ventral view of labrum of Aeshna interrupta lineata;

b) ventral view of labrum of Pantala flavescens.

br - brush; sens - sensillum.

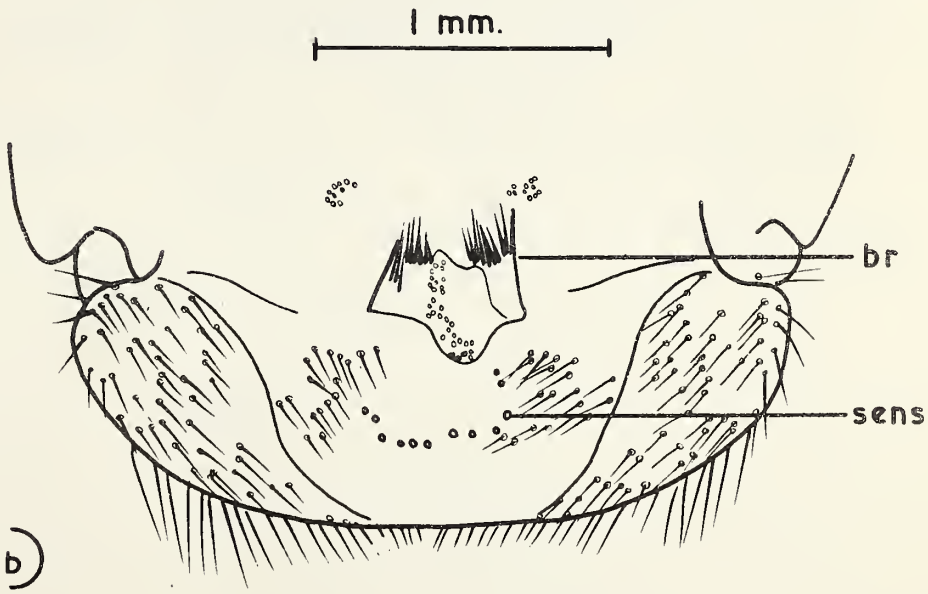
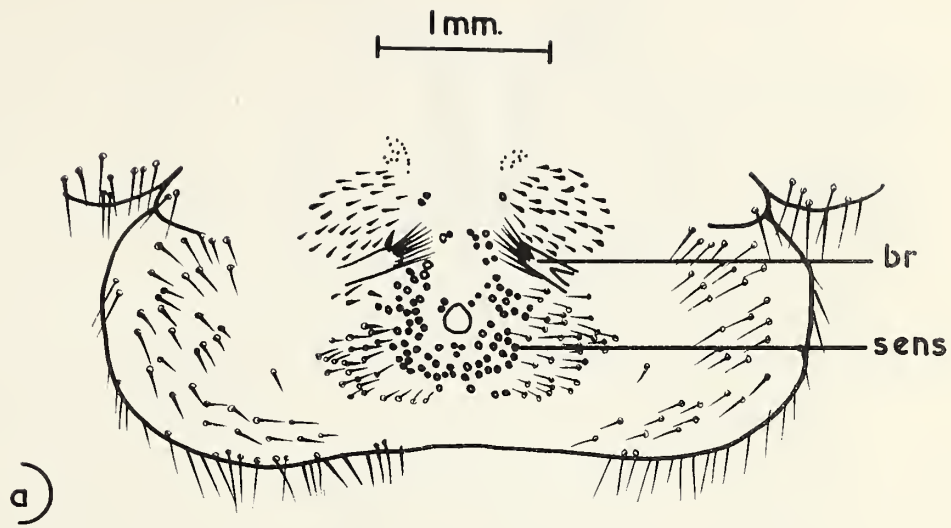


FIG. 19. - The mouthparts of the adult of Libellula
quadrimaculata.

- a) Anterior view of head dissected to show labral muscles;
- b) dorsal view of labium dissected to show muscles.

addlp - adductor of labial palp; eh - end hook; eps -
epistomal ridge; lp - labial palp; lr - labrum; hyp -
basal bar of hypopharynx; mlra - anterior labral
muscles; mlrp - posterior labral muscles; rthyp -
retractor of hypopharynx; 1^ofl, 2^ofl, 3^ofl - primary,
secondary, tertiary flexors of prementum.

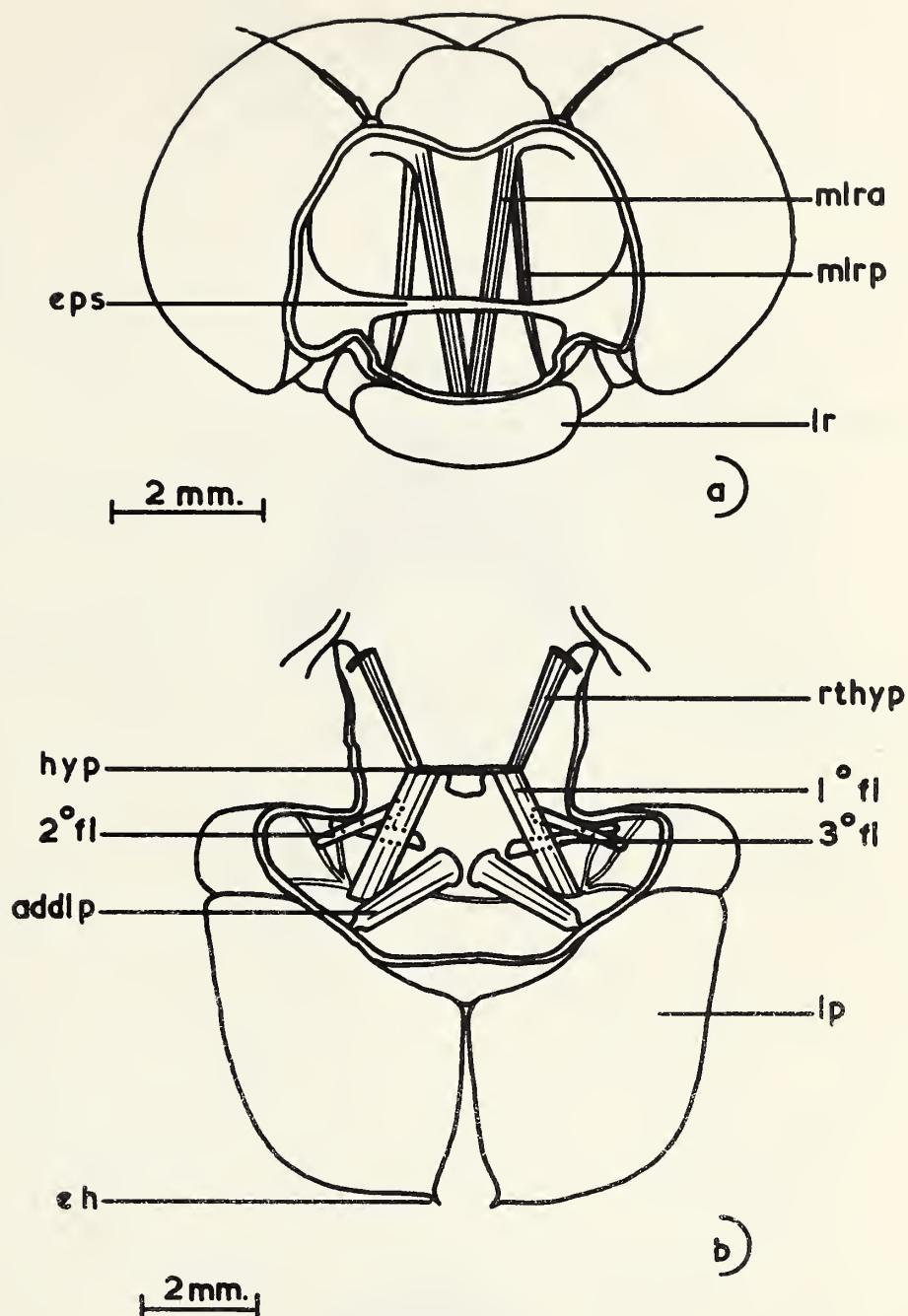


FIG. 20. - The mouthparts of adult dragonflies.

a) Dorsal view of the labium of Aeshna interrupta lineata;

b) dorsal view of the labium of Anax imperator.

eh - end hook; lp - labial palp; mh - movable hook; ml -
median lobe; pag - palpiger; prm - prementum.

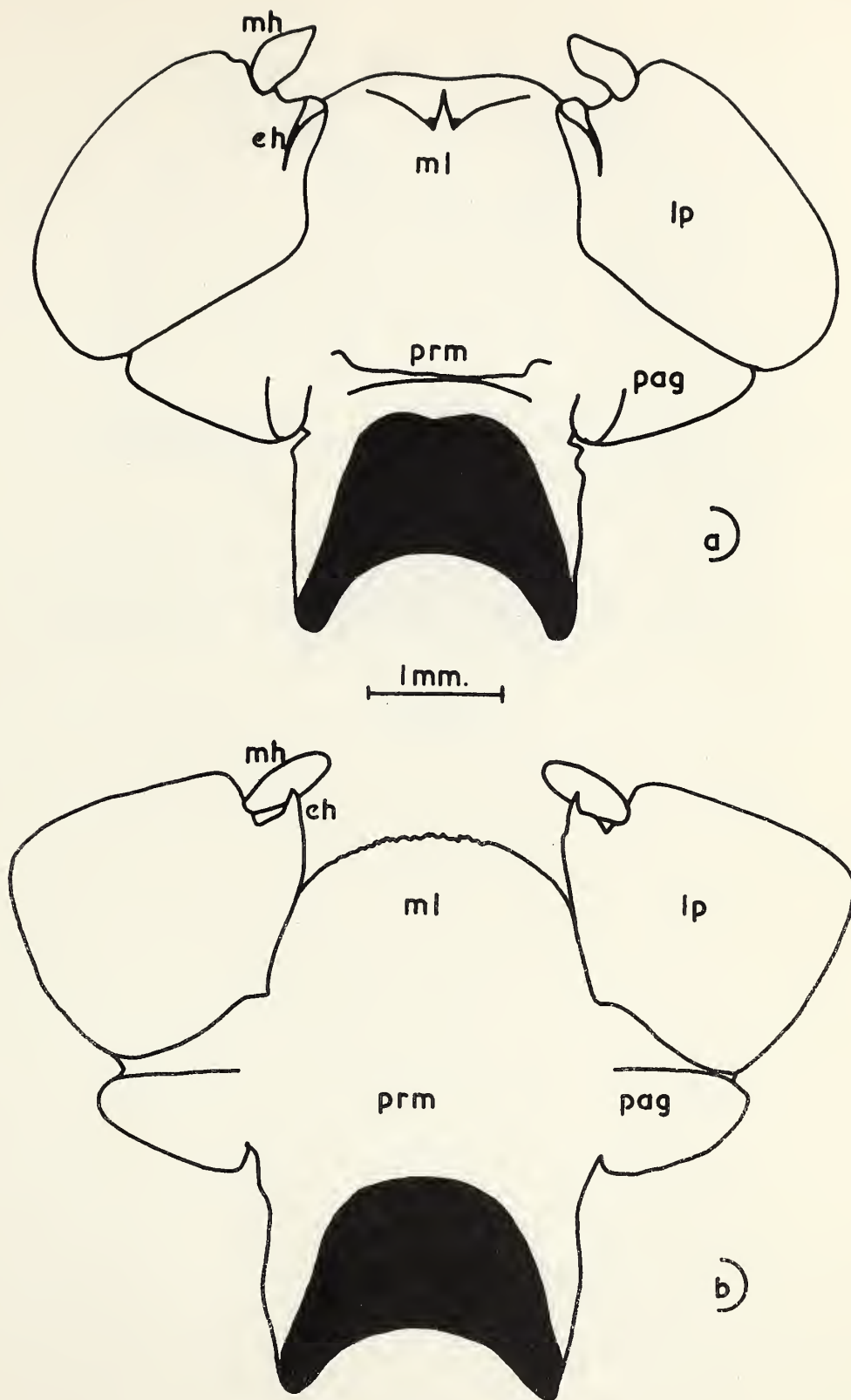


FIG. 21. - Dorsal view of the labium of Cordulegaster
boltonii.

eh - end hook; lp - labial palp; mh - movable hook;

ml - median lobe; pag - palpiger; prm - prementum.

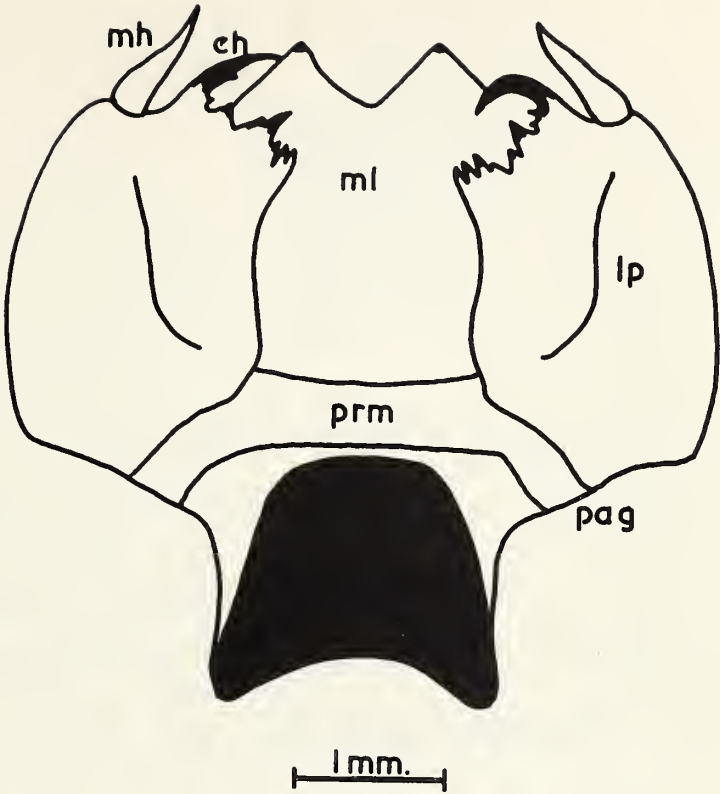


FIG. 22. - The mouthparts of adult dragonflies.

- a) Ventral view of the labium of Allorrhizuca klingi;
- b) ventral view of the labium of Sympetrum striolatum;
- c) ventral view of the labium of Pantala flavescens.

lp - labial palp; ml - median lobe; pag - palpiger;

pom - postmentum.

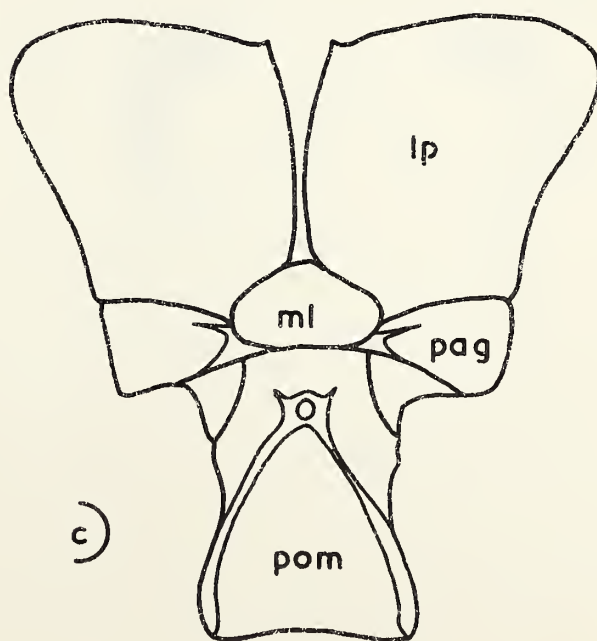
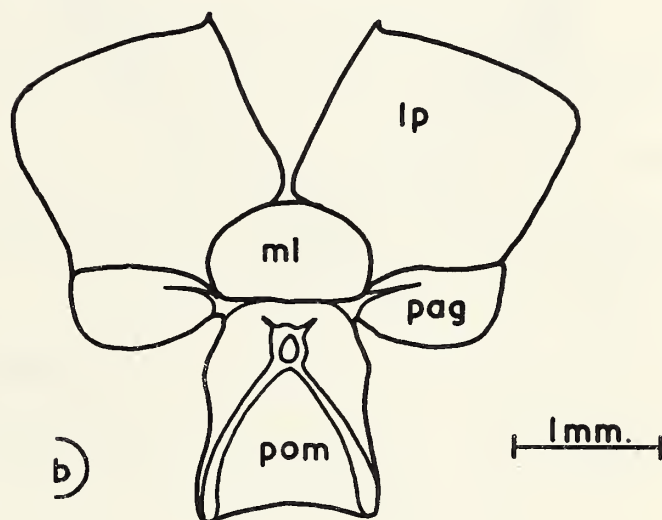
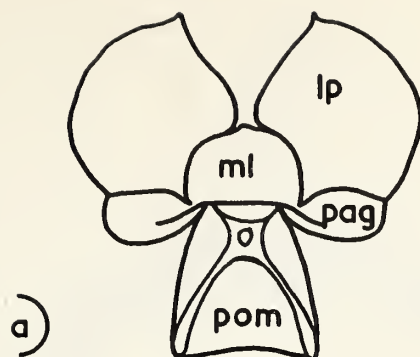


FIG. 23. - Sections through the head of the adult of Aeshna interrupta lineata showing angles of vision.

- a) Transverse-vertical section; each eye covers 208°
and there are angles of binocular vision of 22° above
the head and 34° below the head;
- b) longitudinal-horizontal section; each eye covers 191°
and there is an angle of binocular vision of 22° in
front of the head.

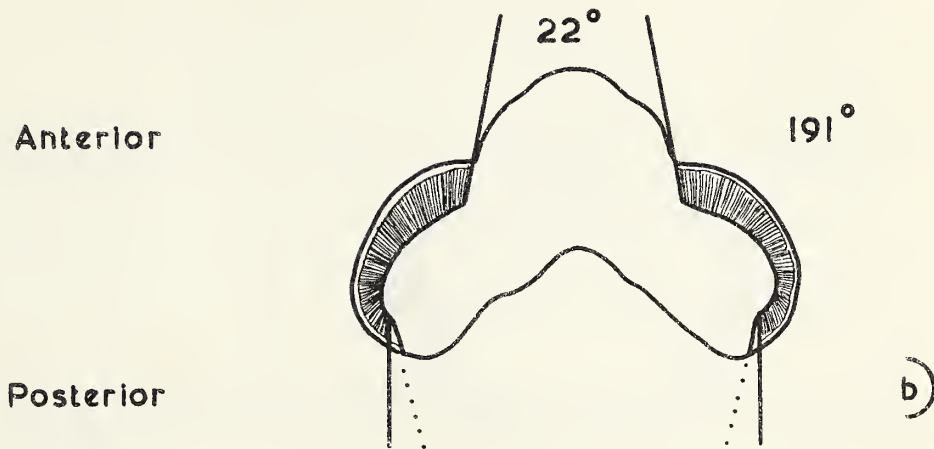
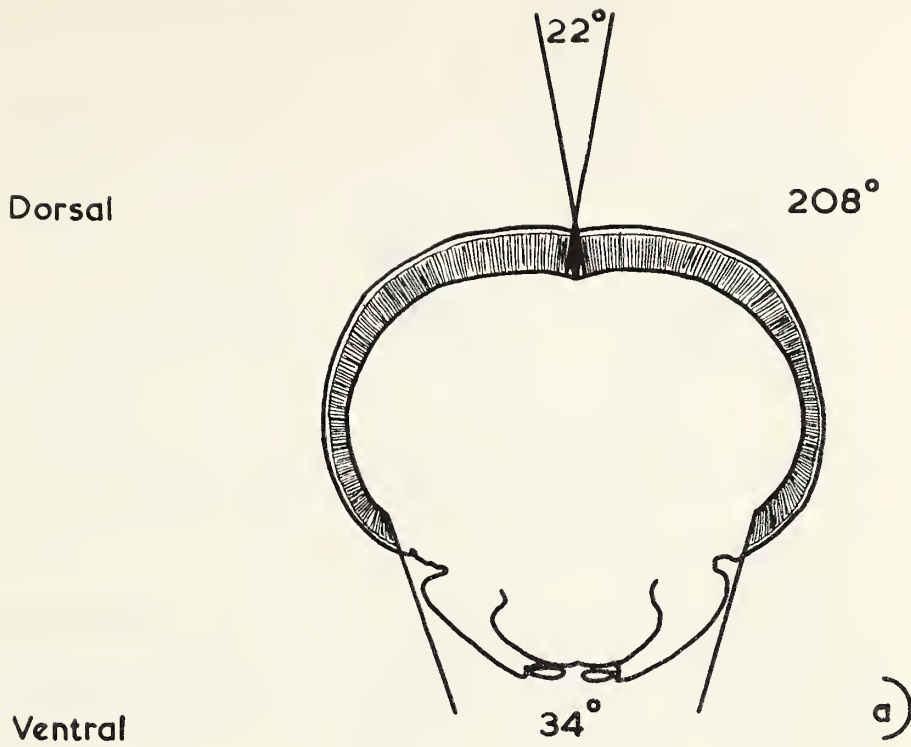


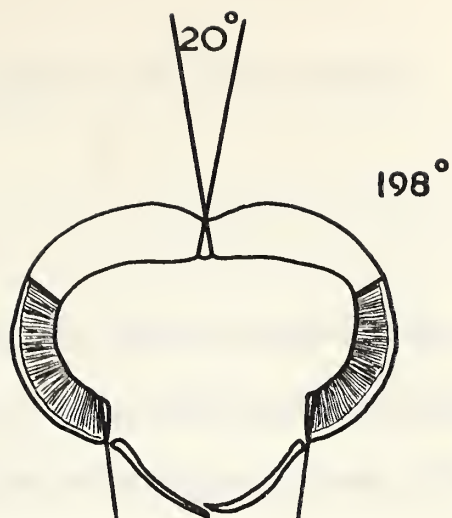
FIG. 24. - Sections through the heads of adult dragonflies showing angles of vision.

- a) Libellula quadrimaculata, transverse-vertical section; each eye covers 198° and there is an angle of binocular vision of 20° above the head;
- b) Libellula quadrimaculata, longitudinal-horizontal section; each eye covers 180° and there is an angle of binocular vision of 20° in front of the head;
- c) Ophiogomphus colubrinus, transverse-vertical section; each eye covers 190° and there is an angle of binocular vision of 14° above the head.

Shaded areas represent pigmented ommatidia.

Dorsal

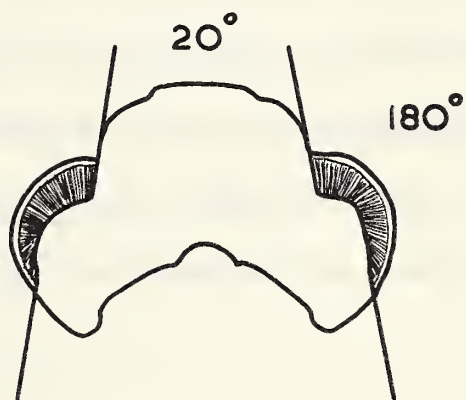
Ventral



a)

Anterior

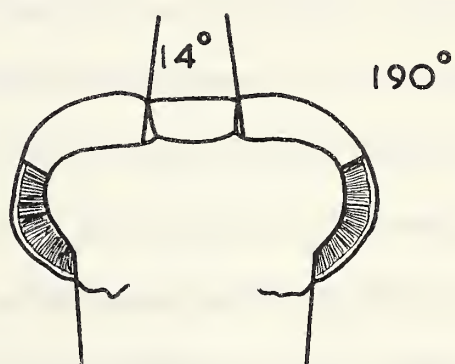
Posterior



b)

Dorsal

Ventral



c)

2mm.

4. SENSE ORGANS ON THE LABRUM

4.1 Introduction

Dragonfly larvae do not eat everything that they catch and the rejection of certain captures after they have been brought to the mouthparts infers that the gustatory sense is well developed. Paper dummies are released almost immediately after capture, but the same dummies soaked in an extract of Tenebrio stimulate chewing for some time. Frings and Frings (1949), experimenting with sugar and ammonium chloride solutions, found adult Libellula sp. difficult to test for the location of chemoreceptors, but they concluded that the mouthparts probably did bear such organs.

The underside of the labrum, or epipharynx, of insects is frequently the site of several types of sensilla. Three main types can be distinguished in dragonflies (Figure 25); articulated hairs more than 100 microns in length (a) are found around the anterior border of the labrum, and just behind these are smaller articulated hairs less than 40 microns in length (b), whilst small unarticulated sensilla (c) are scattered over the body of the hypopharynx. It is these latter sensilla with which this section is concerned.

Zawarzin (1912) investigated the sensilla of Aeshna sp. larva, but made no reference to the cellular components.

4.2 Materials and Methods

Labral sense organs of Aeshna interrupta lineata larvae and adults were investigated. The material was fixed in aqueous Bouin and then was stored in the fixative for several months. The labra were dehydrated in dioxane over anhydrous calcium chloride for 24 hours and were embedded by Peterfi's method of preimpregnation with celloidin. Sections were cut at 7.5 microns and were stained by the Benda-Heidenhain iron haematoxylin method and Mallory's triple stain method. The various layers of the cuticle were identified according to their colour with Mallory's stain (Schatz, 1952).

4.3 The sensilla of the adult (Figure 26, Plate 1)

The cuticle on the dorsal side of the labrum consists mainly of exocuticle (unstained by Mallory's stain) with some mesocuticle (red with Mallory's stain). On the ventral side it consists mainly of mesocuticle and endocuticle (blue with Mallory's stain). The sensilla under consideration are restricted to this more membranous epipharyngeal surface. Exocuticle on the ventral side occurs only around the sense organs; where the sense organs are grouped together, exocuticle surrounds the group as a whole, and when they occur singly, each sensillum has its own exocuticular envelope. Covering each sensillum is a thin layer of mesocuticle (mc), which is in turn covered by exocuticle (ex) for the most part. At the surface, however, the

sensory elements are covered only by the thin mesocuticular layer. Each sensillum has a group of sense cells (scl) in the epidermis and the distal processes (dp) of these cells form a bundle which passes up through the cuticle and attaches to the mesocuticular process. Four fibrils can be seen distal to the sense cells, indicating perhaps that there are four such cells. These fibrils join in pairs and so there are two fibrils which continue to the surface. Four darkly staining bodies (rs) are closely applied to the sensory fibres; these bodies appear to be analogous with the 'Riechstäbschen' described by Vogel (1923). The distal processes are surrounded by a large accessory cell (acl), which is presumably homologous with the trichogen cell of a typical hair sensillum, and each group of sense cells is produced proximally into a nerve fibre (nv) (Plate 2a).

4.4 The sensilla of the larva (Figure 27, Plate 2b)

The cuticle of the dorsal side of the labrum consists, as in the adult, mainly of exocuticle and mesocuticle, with only a thin layer of endocuticle. The cuticle on the ventral side is twice as thick, as that of the adult, but is mainly endocuticle (en), with a thin layer of mesocuticle (mc), and exocuticle (ex) is again restricted to the areas around the sensilla. Each sensillum has a group of sense cells (scl) in the epidermis and processes from these cells unite to form a long, thin distal process (dp) which passes up through the cuticle. At the

surface, the distal process is attached to a very small cuticular projection (cp). Surrounding the distal process is a group of darkly staining granules (rs) which are called 'Riechstäbschen' here, although their arrangement is somewhat different from the more typical form shown by the adult. The distal process is associated with an accessory cell (acl) in its passage through the cuticle.

4.5 Discussion

The morphology of the cuticular sense organs of insects has been discussed by several authors (see e.g. Snodgrass, 1926, 1935; Hsu, 1938), and a classification into hair sensilla, campaniform sensilla, placoid sensilla, and scolophorous sensilla is generally accepted. The function with which each type of organ is connected is, however, not always clear. A thick articulated hair with a single sense cell attached to its base quite evidently serves as a mechanoreceptor. Similarly, organs in which the sense cell is covered only by a very thin cuticle would appear to be structurally fitted for the reception of chemical stimuli. Electro-physiological methods have confirmed these views for some insects.

Organs with a thin cuticular covering are generally associated with a group of sense cells, and it is now generally believed that the presence of a group of cells marks a chemoreceptor

and a single cell marks a mechanoreceptor. Temperature receptors vary but are distinguished from mechanoreceptors by being short and from chemoreceptors by being thick-walled. But this is largely indirect evidence and until more is known of the penetration of the insect cuticle by chemical substances, the exact function of some insect cuticular sensilla must remain in doubt.

It appears that the dragonfly sensilla under investigation are morphologically of a very reduced hair type (reduced basiconic) and that they function as contact chemoreceptors. The morphology of the adult sensilla particularly supports this view. Their position on the epipharynx, the thin mesocuticular cap, and the four fibrils are the main pointers. 'Riechstäbchen' (olfactory rods) were originally described by Vogel (1923) from placoid sensilla on the antennae of bees, but he admitted that olfactory organs may not be the only sensilla to possess these bodies. It appears, however, that they are generally associated with chemoreceptors, although their function is unknown.

The sensilla of larval dragonflies are rather different from those of the adult. The cuticular covering of the sensory process is thin and the small cuticular projection suggests a basiconic structure. However, separate fibrils cannot be distinguished in the distal process and the arrangement of dark granules does not conform to the typical

arrangement of 'Riechstäbchen'. Nevertheless, it seems that several sense cells are involved in the distal process. No dependence of the structure of the sensilla on the media in which the larva and adult live could be seen, although the reception of stimuli will be different in the two media and the differences in the structure of the sensilla may be attributable to this.

FIG. 25. - Surface view of the ventral side of the labrum of the larva of Aeshna interrupta lineata.

a - articulated hairs more than 100 microns in length;

b - articulated hairs less than 40 microns in length;

c - gustatory sensilla;

ex - exocuticle.

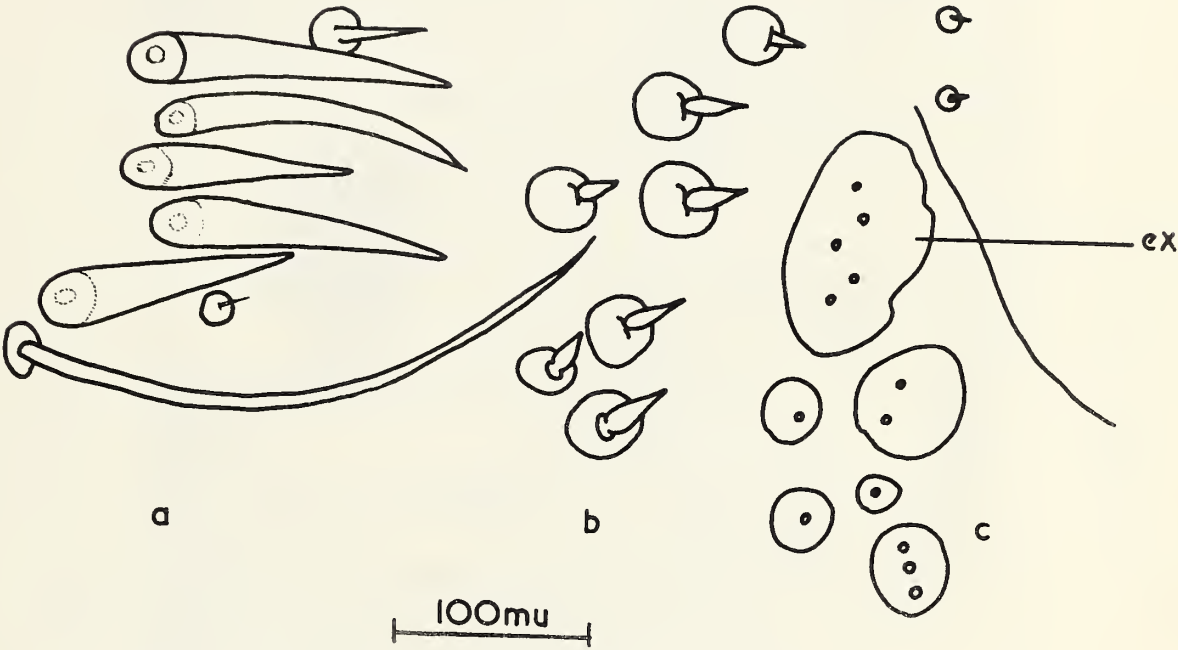


FIG. 26. - Gustatory sensilla in the labrum of the adult of Aeshna interrupta lineata.

acl - accessory cell; bm - basement membrane; dp - distal process;

en - endocuticle; epd - epidermal cell; ex - exocuticle;

mc - mesocuticle; nv - nerve; rs - Riechst bschen; scl - sense cells.

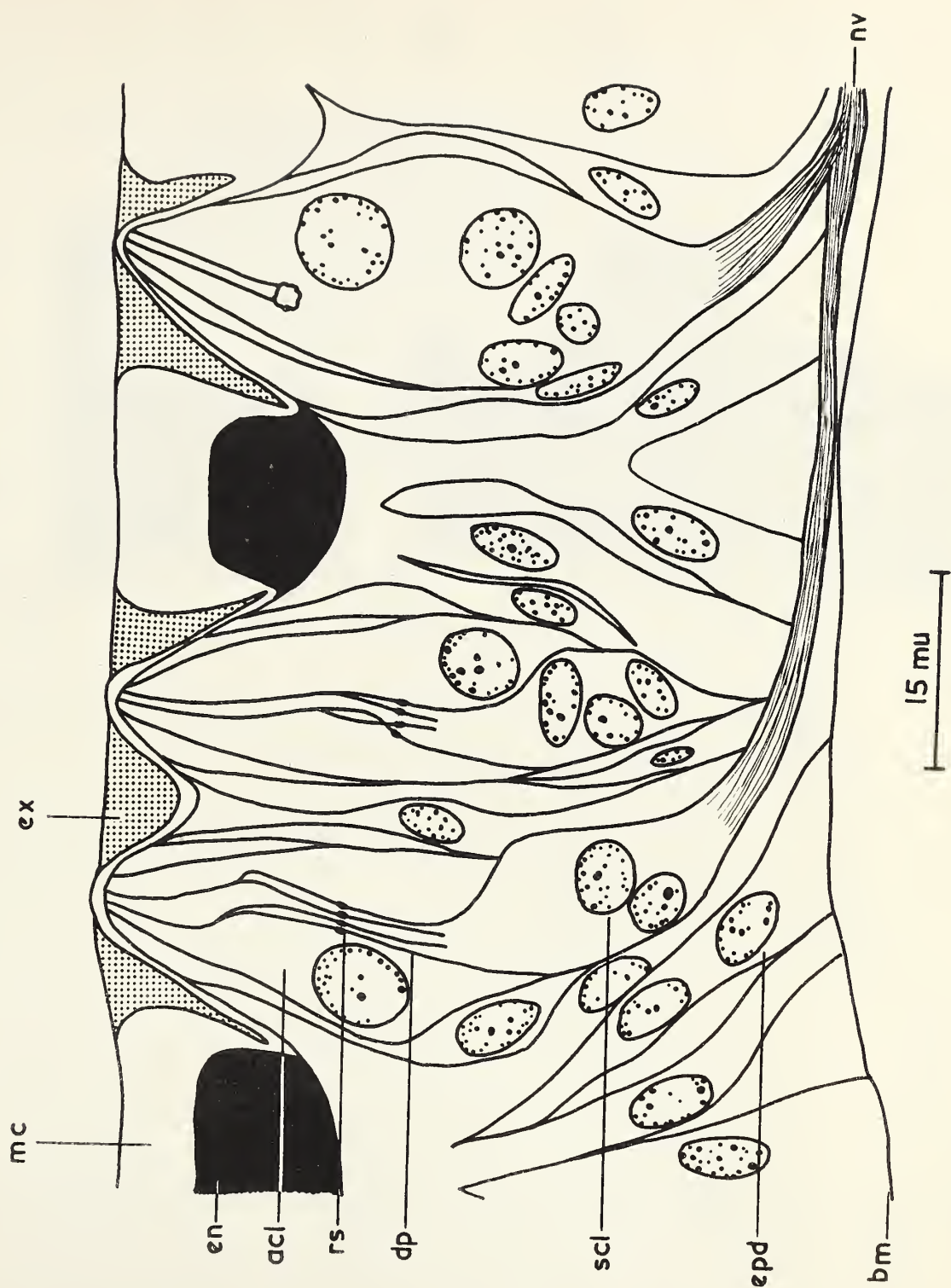


FIG. 27. - Gustatory sensillum in the labrum of the larva of

Aeshna interrupta lineata.

acl - accessory cell; cp - cuticular process; bm - basement
membrane; dp - distal process; ex - exocuticle; en - endo-
cuticle; epd - epidermal cell; mc - mesocuticle;
rs - 'Riechstäbschen'; scl - sense cell.

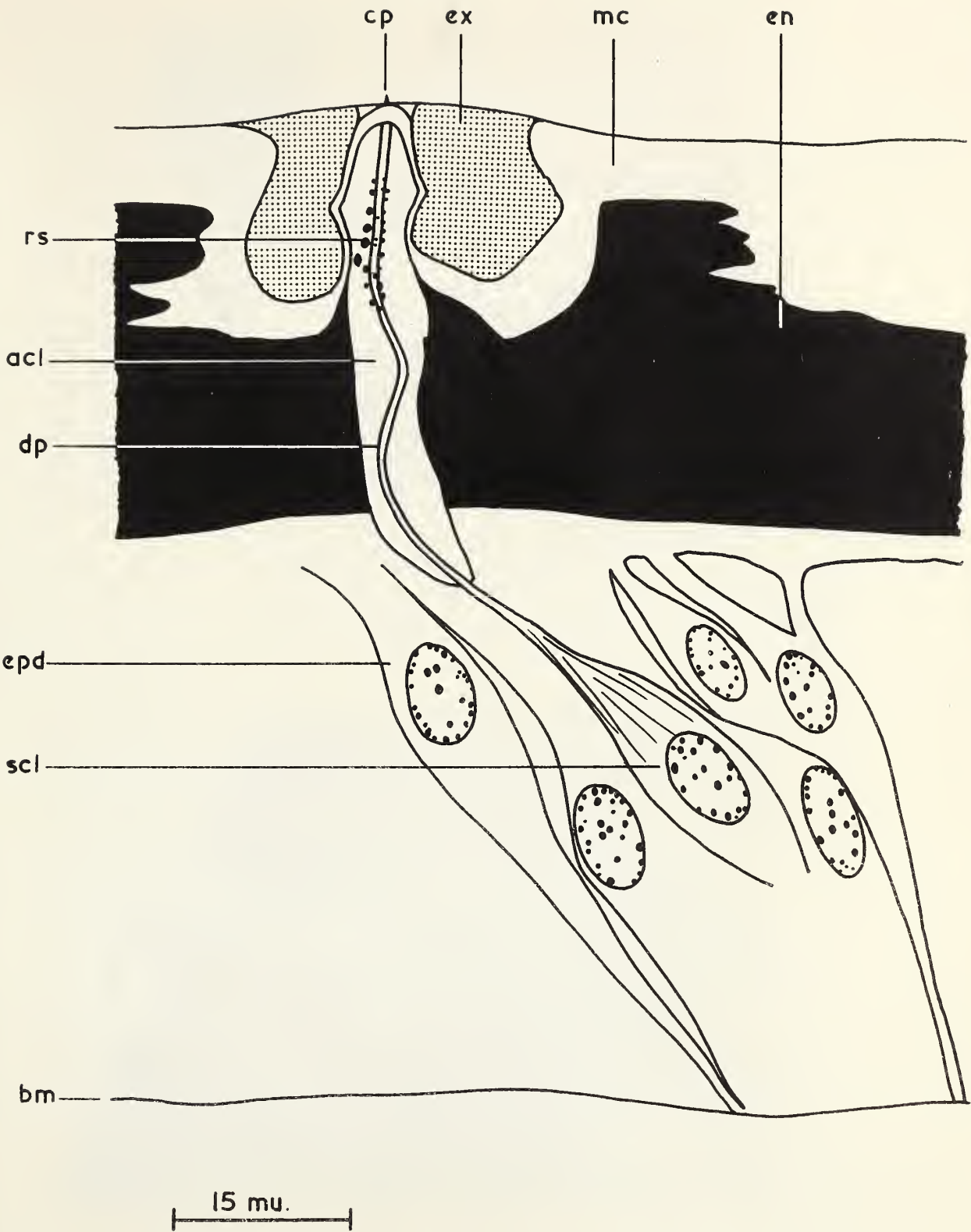
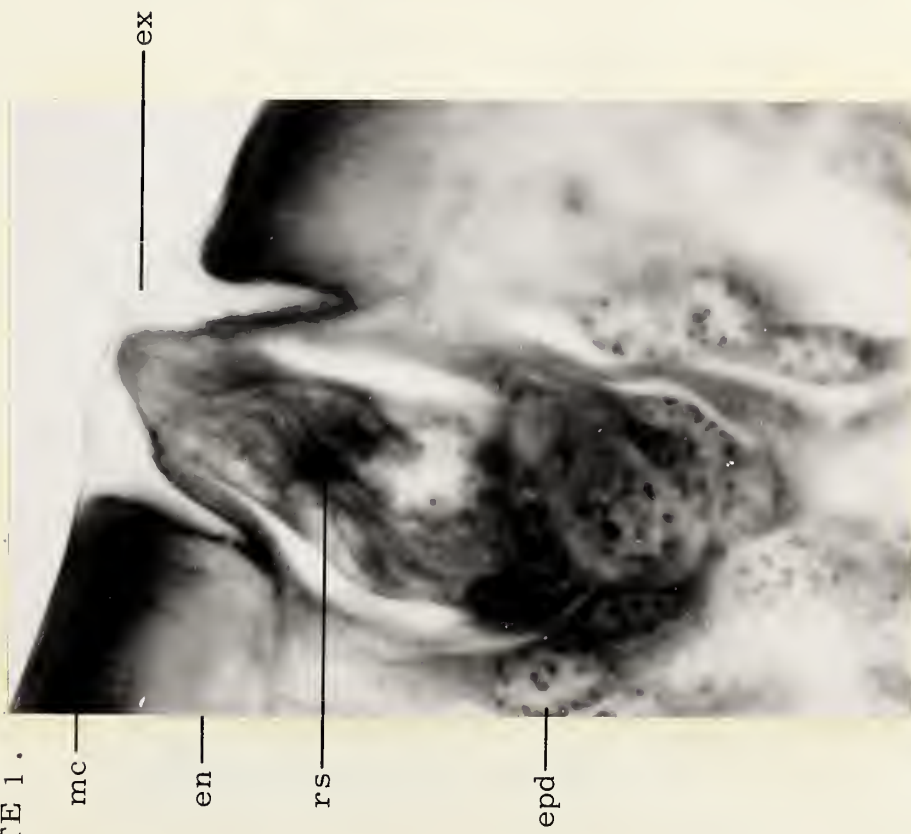


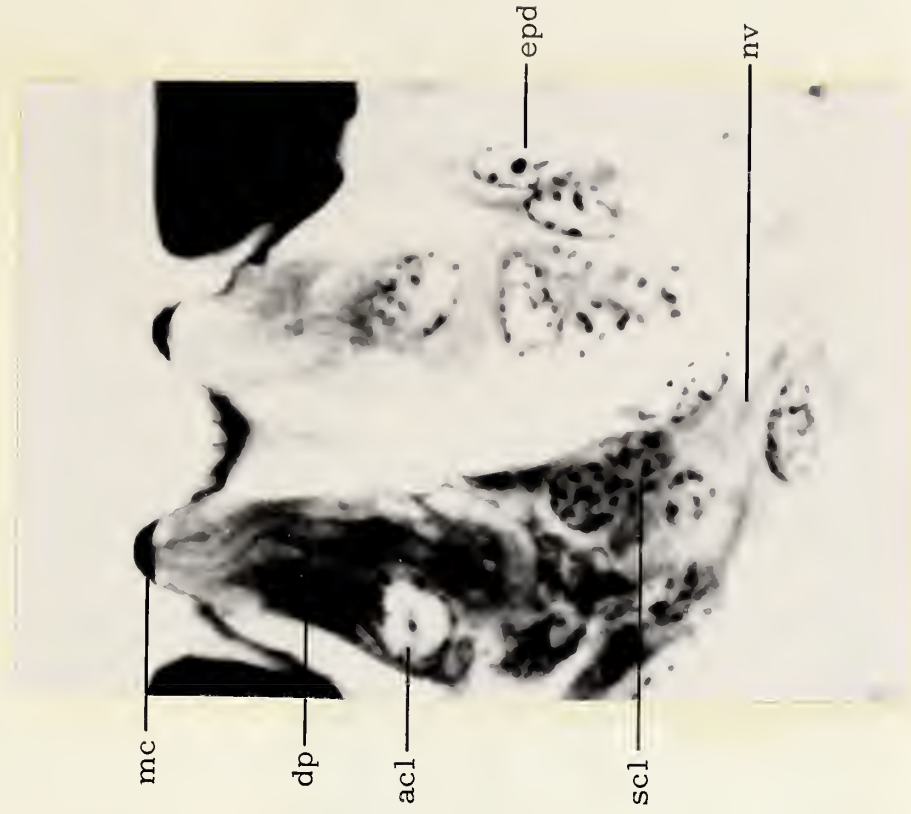
PLATE 1. - Sensilla in the labrum of adult Aeshna interrupta lineata.

- a) Mallory's triple stain;
- b) Benda-Heidenhain iron haematoxylin stain.
 - acl - accessory cell; dp - distal process;
 - en - endocuticle; epd - epidermal cell;
 - ex - exocuticle; mc - mesocuticle; nv -
nerve fibre; rs - Riechstäbchen; scl -
sense cells.

PLATE 1.



a)



b)

15 μ m

PLATE 2. - a) Nerve fibre from sense cells of sensillum of
adult Aeshna interrupta lineata.

bm - basement membrane; nv - nerve fibre;

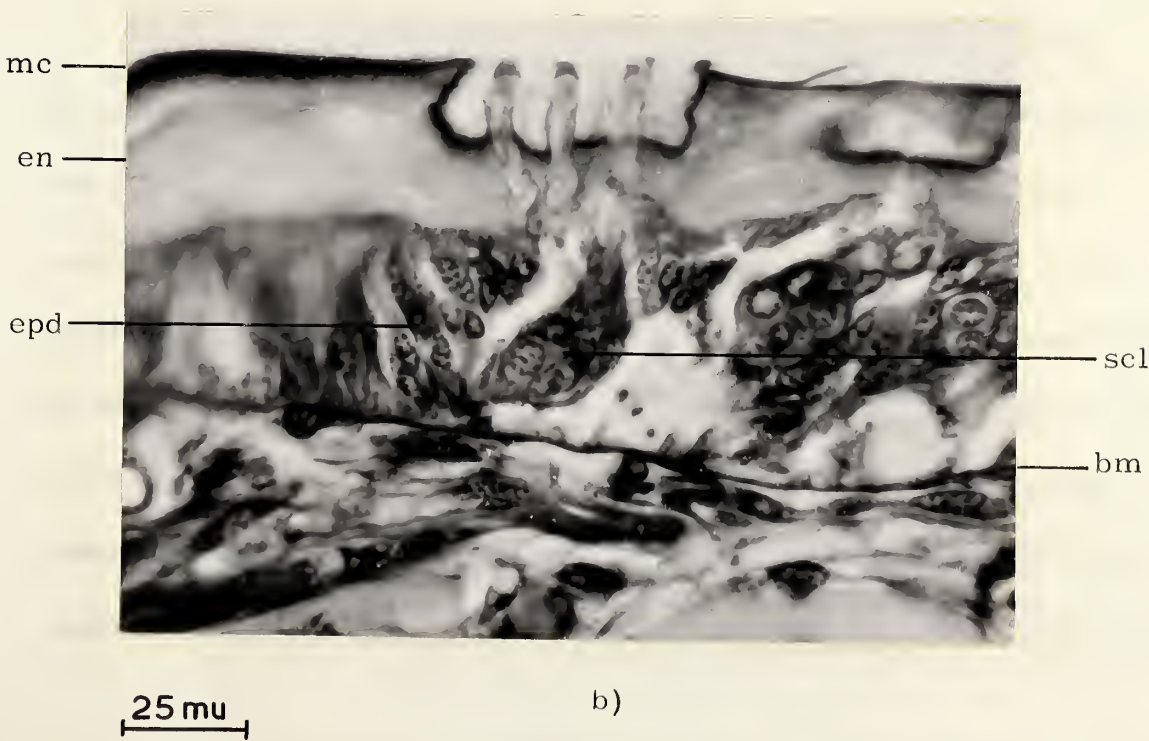
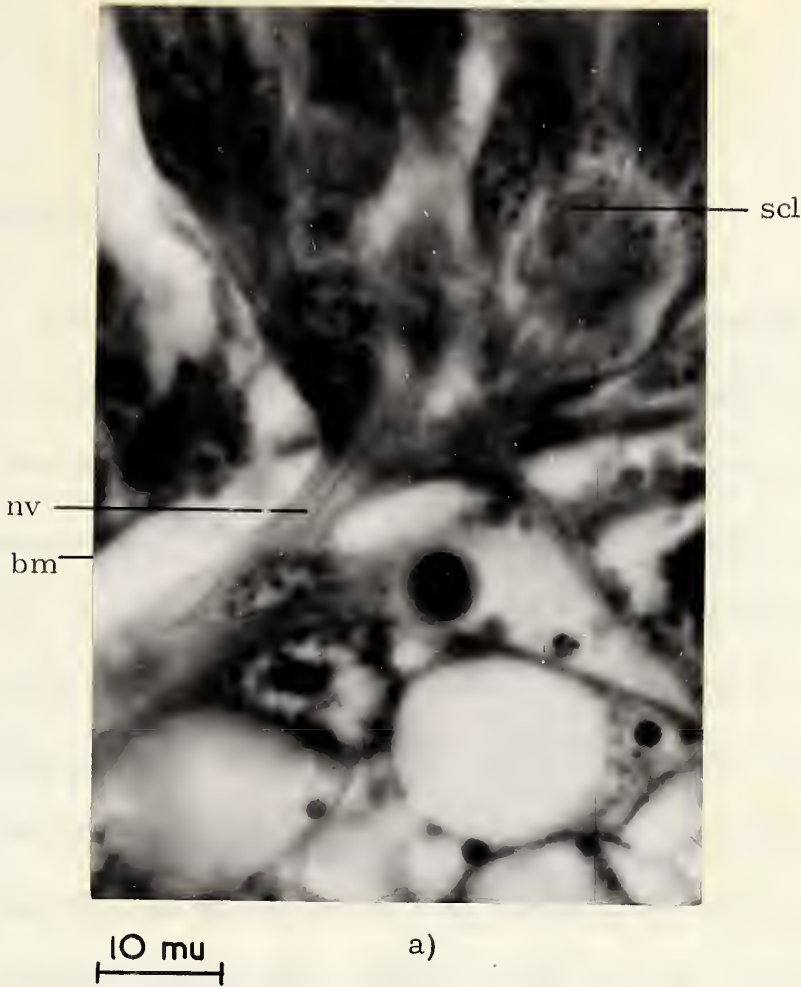
scl - sense cell.

b) Sensilla in the labrum of the larva of Aeshna
interrupta lineata.

bm - basement membrane; en - endocuticle;

epd - epidermal cell; mc - mesocuticle;

scl - sense cells.



5. THE PREY OF DRAGONFLY LARVAE

5.1 Introduction

Several reports on dragonfly biology carry some remarks on the food of larvae. Many of these emphasize the voracity of larvae in the laboratory, some give isolated observations on natural prey, and others unqualifyingly accept ^{the} _A view that the diet contains most forms of aquatic life. It is the aim of this study to present the first systematic enquiry into the natural food of Anisopteran dragonfly larvae, with a view to determining what animals form the food of these insects, whether there are any food preferences, whether the food taken by larvae of different species can be related to their habits, if there is any relation between the food and the size of the dragonfly larvae, and whether there is any significant variation in the food at different times of the year.

It is evident from the experiments of Warren (1915) that dragonfly larvae will eat a wide range of animals presented to them in the laboratory. Hinman (1934) has given impressive figures for the consumption of mosquito larvae by Pantala flavescens Fabr. in the laboratory, but as Wright (1946) has pointed out these experiments only emphasize the voracity of dragonfly larvae and bear little relation to their food under natural conditions. Clausen (1940) reports that dragonfly larvae feed on Crustaceans, tadpoles, small fish and aquatic insects. Kasimov (1956) records Anax imperator Leach larvae feeding

on Oligochaetes, Chironomid larvae and other insects, tadpoles, frogs, fry and spawn of herring, and Ostracods, with ticks, mites and green algae also found in their intestines. Needham and Hart (1901) remark that Anax and Epicordulia larvae live for the most part on Molluscs, the former even feeding on thick-shelled Amnicola. The damage caused by dragonfly larvae in fish hatcheries has been reviewed by Wright (1946), who agrees with Wilson (1918) that only certain of the larger species are concerned with the destruction of young fish, but emphasizes that these few are capable of considerable economic damage and control measures may be necessary.

The most complete record of the natural food of dragonfly larvae to date is that of Warren (1915) who examined the gut contents of 253 Anax and Pantala larvae in Hawaii. His results show Chironomid larvae and Ostracods to be the commonest components of the diet. The few records of mosquito larvae as prey are explained by the fact that of the many localities collected from only two contained these insects, but in these two habitats fully half of the dragonfly larvae had mosquito larvae in their alimentary canals.

5.2 Methods

The food of dragonfly larvae is broken up by the mouthparts and is then stored for some time in the crop before passing slowly through the gizzard. The gizzard has only a little effect on the larger

chitinous pieces but it grinds up the softer material and so allows for more efficient enzyme action in the mid-gut. The peritrophic membrane is produced by delamination from the mid-gut epithelium (Voinov, 1898; Aubertot, 1932) and production and elimination continue even in the absence of food. Undigested materials pass quickly through the hind-gut, presumably so that they do not interfere with colonic respiration, and they are voided enclosed in a strong envelope of peritrophic membrane. Examination of the contents of these faecal pellets provides the most convenient method for the analysis of the food of dragonfly larvae in nature.

Larvae were collected from several habitats each week throughout the season. In each habitat, an area in which there was little physical and floral variation was used for the collection of each week's sample. Dragonfly larvae were collected with a hand net and at the same time a rough estimate was made of the abundance of animals that may have served as prey and which had been collected by the same method. The dragonfly larvae were identified, measured from the front edge of the labrum to the tip of the anal siphon, and confined in separate jars until they had emptied their alimentary canals. The contents of their faecal pellets were then examined under the microscope and recorded.

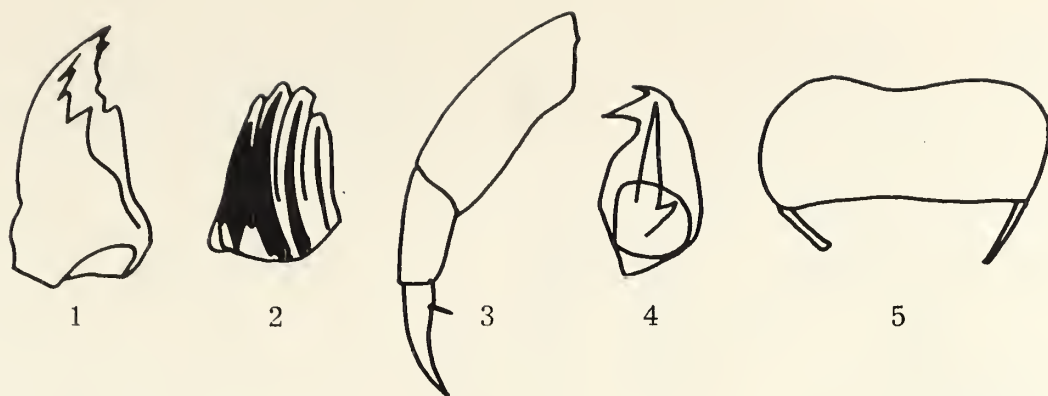
This method of food analysis depends on the prey having some easily identifiable hard parts that are not digested and will appear in faecal pellets. This is so with most prey animals (Figure 28), but

FIG. 28. - Remains of prey found in faecal pellets of dragonfly larvae.

Trichoptera larvae: 1. Mandible; 2. Mandible; 3. Leg;
4. Abdominal hook; 5. Labrum.

Zygoptera larvae: 6. Labial palp; 7. Labial palp;
8. Lacinia; 9. Mandible; 10. Part of antenna; 11. Part
of femur.

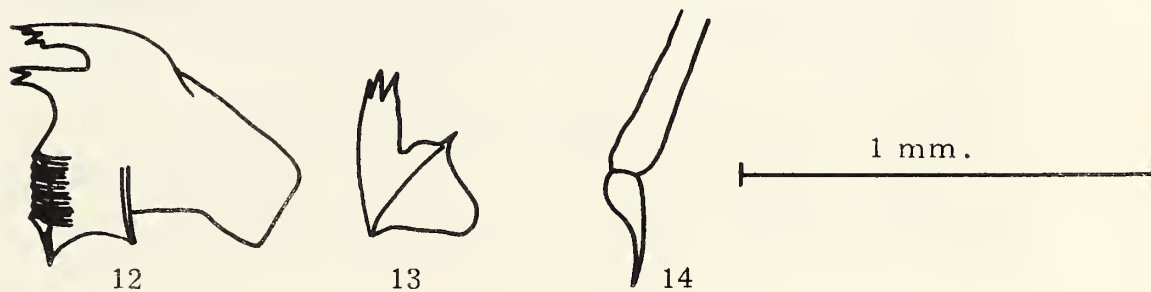
Ephemeroptera larvae: 12. Mandible; 13. Part of mandible;
14. Part of tarsus.



Trichoptera larvae.



Zygoptera larvae.



Ephemeroptera larvae.

FIG. 28. - cont'd.

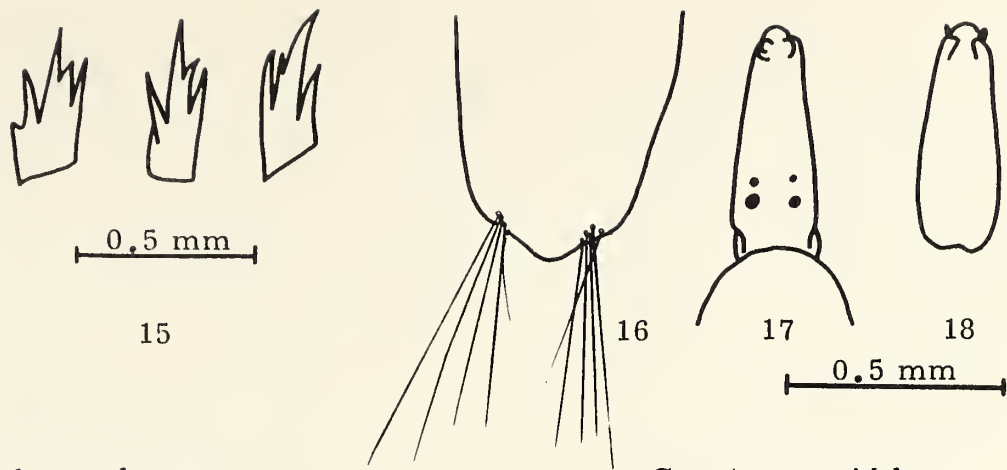
Chaoborus larvae: 15. Mandibles.

Ceratopogonid larvae: 16. Hind end; 17. Head; 18. Head.

Chironomid larvae: 19. Head capsule with submentum;
20. Mandible; 21. Proleg spines.

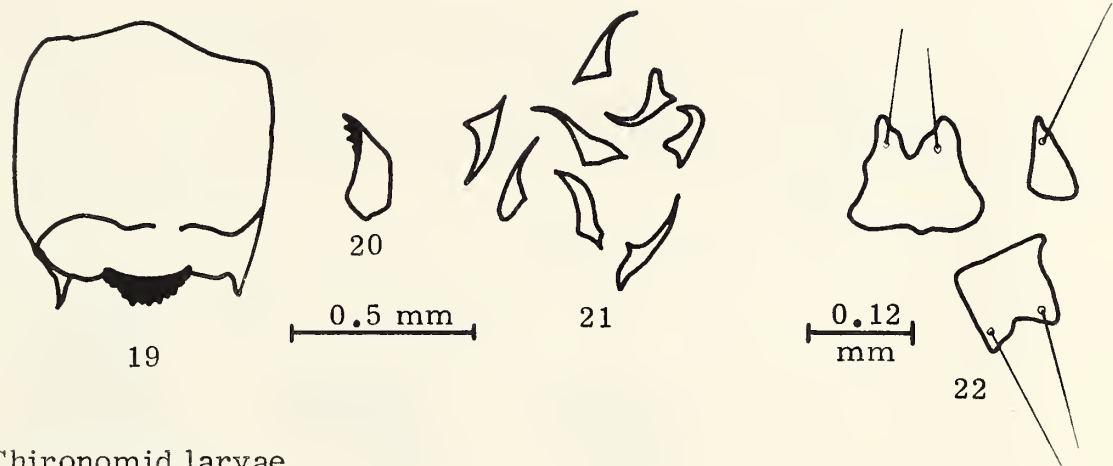
Chironomid pupae: 22. Abdominal projections.

Culicine larvae: 23. Group of setae; 24. Submenta;
25. Parts of respiratory siphons; 26. Mandible.



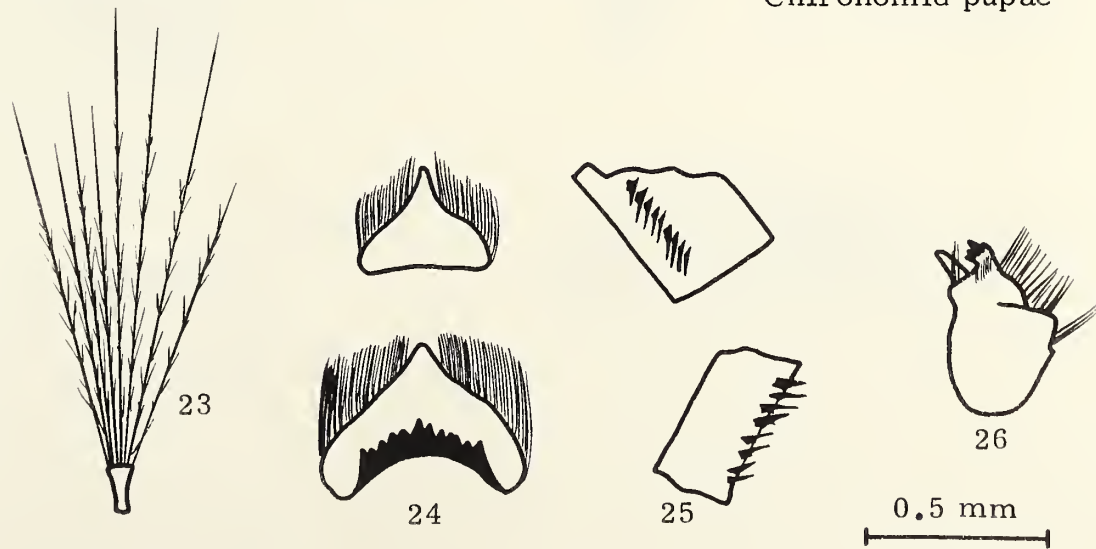
Chaoborus larvae

Ceratopogonid larvae



Chironomid larvae

Chironomid pupae



Culicine larvae

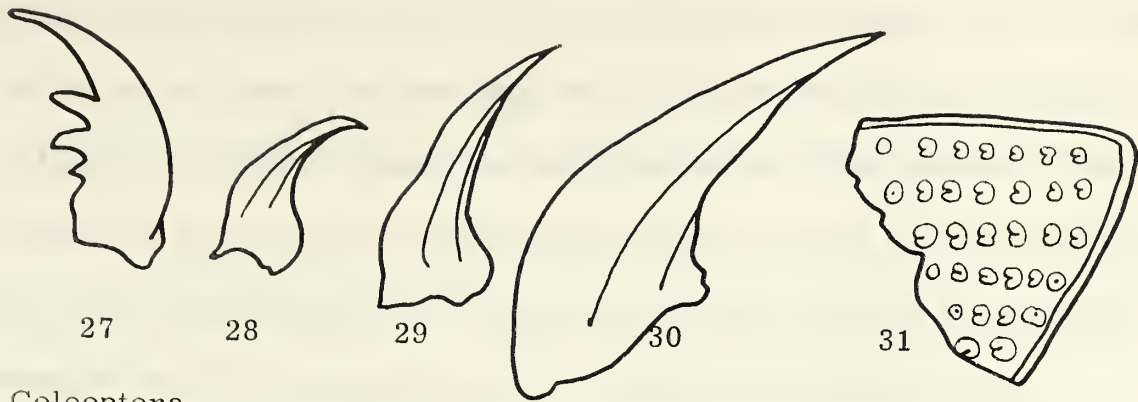
FIG. 28. - cont'd.

Coleoptera: 27-30. Mandibles; 31. Part of elytron.

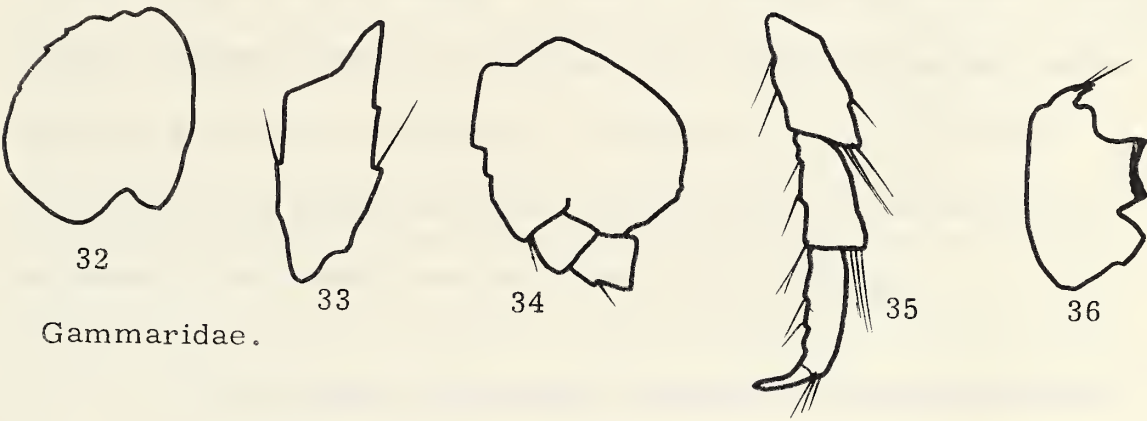
Gammaridae: 32-35. Parts of legs; 36. Mandible.

Mollusca: 37-39. Parts of Gastropod shells.

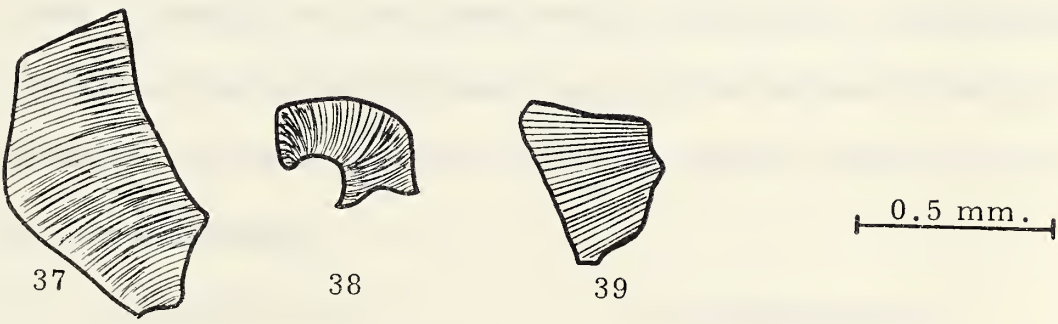
Aerial Insects: 40-41. Wings.



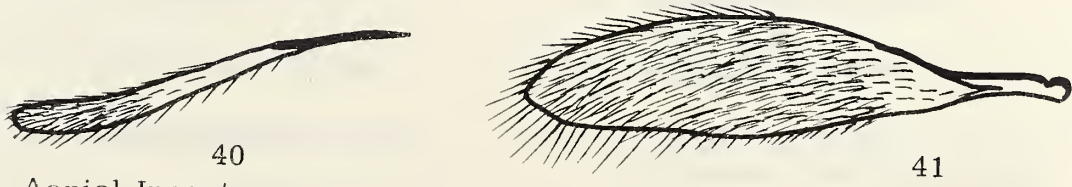
Coleoptera.



Gammaridae.



Mollusca



Aerial Insects.

completely soft bodied forms such as annelids are missed, and when only soft parts are eaten, as often may be the case with molluscs, these too will pass unnoticed. Dissection and examination of the contents of the alimentary canal may yield more information on these soft-bodied forms but an accurate estimation of their role as food could only be obtained through the use of precipitin tests, which are impractical when considering the whole range of prey of a particular predator. Analysis of faecal pellets produces almost as much information as gut content analysis and has the advantages of being much quicker and more convenient, and furthermore the larvae are not harmed and can be returned to the habitat from which they were collected.

The remains of the prey could often be identified only to order or family, but this rather broad classification was thought not to conceal any facets of prey selection. For the purpose of analysis the prey that was found in faecal pellets was grouped under the following seventeen headings:

- | | |
|-------------------------|---|
| 1. Chaoborine larvae | 10. Trichoptera larvae |
| 2. Chironomid larvae | 11. Anisoptera larvae |
| 3. Chironomid pupae | 12. Zygoptera larvae |
| 4. Ceratopogonid larvae | 13. Small Crustacea
(Cladocera and Ostacoda) |
| 5. Culicine larvae | 14. Gammaridae |
| 6. Coleoptera larvae | 15. Hydracarina |
| 7. Coleoptera adults | 16. Mollusca |
| 8. Corixidae | 17. Aerial Insects
(Non-aquatic forms) |
| 9. Ephemeroptera larvae | |

In Section 5.3 the animals that were thought to qualify under the heading of 'potential prey' are identified to genera and the broader classification used in the analysis will encompass these genera only.

A consideration of the effect of dragonfly larvae on the trophic structure of the environment would demand an estimation of the relative masses or volumes of the various components of the diet. But as this study is primarily concerned with the selection of prey by the dragonfly larva, the method of 'frequency of occurrence' gives sufficient information, as well as being substantially easier to apply to a carnivorous diet than any method involving a counting or points system. In this method, the number of dragonfly larvae in which each prey animal occurs, is recorded as a percentage of the total sample. It should be remembered that the results given here do not give an accurate estimate of the amount that is contributed to the food by each type of prey, although investigations on the food of fishes have shown that, except with very small prey, all methods, whether using the volume, numbers or frequency of occurrence of the prey, yield comparable results (Hynes, 1950; Ball, 1961). The frequency of occurrence method is generally successful in indicating the order of importance of items in the diet. For a full description of the methods used in the analysis of gut contents see Hynes (1950).

Larvae that are undergoing metamorphosis to the adult and those that have recently moulted do not feed, and in order that larvae in

these states should be excluded from the analysis the results were tabulated only from those larvae that had eaten. These results are shown in Figures 29-34.

5.3 Habitats

In the spring, there is a wide variety of aquatic habitats in central and northern Alberta. In addition to the more or less permanent lakes and ponds, low-lying ground and depressions everywhere are filled with water from the melting snows. Many of these habitats are of a temporary nature and are unsuitable for habitation by dragonfly larvae. Other large areas are prevented from drying up completely by a dense mat of sedges and mosses growing on a thick bed of decaying vegetation. These large areas of swampy ground, which go under the popular name of 'muskeg', have little open water and their Odonate fauna is generally scanty. The edges of clean, permanent waters with healthy vegetation are the most suitable habitats for dragonfly larvae.

Larvae were collected from ponds in the vicinity of Edmonton in 1961, and from lakes and ponds in the Flatbush area, 100 miles north of Edmonton, in 1962. The almost complete absence of dragonfly larvae from lotic waters in the study areas has meant that this important habitat-type has been neglected. The study of the food of larvae, especially burrowing forms, living in streams and rivers, would make a valuable comparison with the data obtained here from

static bodies of water.

5.31 Habitats in the Flatbush area

The spring and summer of 1962 were spent in the community of 'Athabina' (54°37' - 54°42' N, 114°11' - 114°18' W), seven miles west of the village of Flatbush and lying between the Athabasca and Pembina rivers. The area lies on the border of the parkland and the boreal forest and is dominated by forests of aspen poplar (Populus tremuloides Michx.), with some balsam poplar (P. balsamifera L.) and spruce (Picea glauca (Moench)). Athabina has been fairly extensively cleared for farming purposes, but large woods, areas of muskeg, and many lakes and ponds have remained unchanged. A fuller description of the area is given by Happold (1963).

Heavy snow in the winter of 1961-1962, and above-average precipitation during the summer of 1962, maintained high water levels in all habitats throughout the season. In all habitats at the time of sampling the pH lay between 5 and 6.

a. Roadside Ditch (Plate 3)

This was a small body of water, 40 m. x 5 m., on the south side of an east-west road. Dragonfly larvae were found only at the western end where there was a good growth of Carex rostrata Stokes and Typha latifolia L. The banks rose steeply and were covered mainly by Carex and various grasses, with a few, low Salix bushes. The water

surface was quite open and the sampling station received no shade during a sunny day. The bottom was muddy and the water was often cloudy due to the influx of water from a similar, higher ditch to the west, and runoff from the gravel road.

Zygoptera (mainly Lestes dryas Kirby and Ischnura sp.) were common during the whole summer. Limnephilid Trichoptera were very common in May and June but few were found after the beginning of August. Coleoptera adults (Haliplus sp., Laccophilus sp., Dytiscus sp.) were common from April to August, and larvae (Dytiscus sp., Hydaticus sp., Graphoderus sp.) were commonly found after mid-July. Of the aquatic Diptera, Chaoborus sp. larvae were common in August, Chironomid larvae from mid-July on, and a few larvae of a Ceratopogonid (Palpomyia sp. or Bezzia sp.) were found in June and July. This habitat contained no mosquito larvae. Ephemeroptera larvae (Siphonurus sp.) were very common in late June and early July but their numbers had diminished by August. No Gammarids were present but smaller Crustacea were quite common in the second half of the season. A few Notonecta spp. were found in June and July and a few Corixa sp. in July and August. Molluscs (Planorbis sp. and Limnea sp.) were common in May and continued in low numbers for the duration of the sampling period and Oligochaete worms were present in the bottom mud.

The Anisopteran fauna was quite sparse and consisted mainly

of Aeshnids (Aeshna interrupta lineata, A. eremita Scudder and A. juncea L.).

b. Watt's Pond (Plate 3)

The sampling at this pond was on the north side amongst thick moss and Carex. The open water occupied a circular area about 50 m. in diameter, and the area for some distance around was soft muskeg and very wet. A band of Carex sp., interspersed with small swamp birch (Betula pumila glandulifera L.) and Salix sp., bordered the pond, and about 10 m. from the open water Menyanthes trifoliata L. was common, with some Triglochin maritima L. and Eriophorum angustifolium Roth. The bottom was soft and largely moss-covered, overlying a great depth of dead vegetation, and by mid-June there was abundant algal growth. Surrounding the pond was thick swamp birch bush, which was, however, quite low so that the pond was exposed and received no shade when the sun was up.

Coleoptera adults (Dytiscus sp., Laccophilus sp. and Haliphus sp.) and larvae (Dytiscus sp., Hydrophilus sp., and Hydaticus sp.) were common at all times. Corixa sp. was also common from May to August and Gerris sp. was found on the water surface. Ephemeroptera (Siphonurus sp.) were common in mid-June but had become rare by the end of July. Chironomid larvae were common in the early summer months and became very common in July and August, whilst pupae were common in June and July. A few Chaoborus sp. larvae were found

at the end of the season and Ceratopogonids were present in low numbers in May and again in July. Two peaks of larval mosquito population were evident; one in June was due to Culex territans (Walker), and one in August was due to Anopheles earlei Vargas. Trichoptera (Limnephilus sp.) showed a peak in May but were not found in the sampling area after this time, whilst Zygoptera (Coenagrion resolutum (Hagen), Lestes disjunctus Selys, and Ischnura sp.) were abundant in May and remained common throughout the season. Molluscs (Planorbis sp.) were also taken in all samples but in low numbers. Gammarus sp. was common and small Crustacea, especially Cladocera, were very common from mid-June onwards.

Leucorrhinia hudsonica Selys was generally common for the whole summer and Sympetrum spp. occurred regularly in samples from July and August. Aeshna canadensis Walker was common, especially in April, May and June.

c. Lake Sara (Plate 4)

Dragonfly larvae were collected from the emergent vegetation zone on the north-east side of this, the largest lake in the area. The edge of the lake in this region had a thick border of emergent vegetation consisting mainly of tall Carex rostrata. Calla palustris L. was common by the bank and Menyanthes trifoliata, Equisetum limosum L., E. arvense L., Calamagrostis canadensis (Michx.), Typha latifolia, Sagittaria cuneata Sheld. and clumps of

Juncus sp. were interspersed through the Carex. There were small amounts of algal growth and Utricularia vulgaris L. in the water and a little Lemna sp. on the surface. The sampling station was overhung by birch, aspen and Salix trees, which afforded shade until about 1000 hours and shed their leaves into the water in the autumn. The substrate was soft and composed mainly of dead Carex and aspen leaves.

Chironomid larvae became common at the beginning of June and remained so throughout the summer; pupae first appeared at the same time and rose to a peak in mid-June. Ceratopogonid larvae appeared in mid-May and were common in June, but were not found after mid-July. No Culicids were found in the sampling area. Adult Coleoptera remained common throughout the season; larvae (Hydrochara sp., Dytiscus spp., and Hydaticus sp.) appeared later, in mid-May, and were common in all samples taken after this time. Corixa sp., either as larvae or adults, was taken regularly but in rather low numbers, whereas Notonecta spp. appeared in large numbers in the sampling area in June, but none were found after the first week of July. Trichoptera were common only in May and a few Ephemeroptera (Siphonurus sp.) occurred at the end of July. Zygoptera (Nehalennia irene (Hagen) and Coenagrion resolutum) were very common in May and June but none were found after mid-July, whilst Molluscs (Planorbis sp.), which were in fairly low numbers during the early part of the summer, increased markedly in July. Small Crustacea appeared at the end of May and were common until August, but the larger Gammarids,

which had been common in the first half of the season, were not found after the first week of July.

The dragonfly larva fauna in the sampling area consisted predominantly of Libellulids; Leucorrhinia hudsonica was common throughout the season and the most of the Libellula quadrimaculata used in the analyses were collected from this habitat after mid-July.

d. Scaup Lake (Plate 4)

The area around this lake consisted mainly of a Carex-moss-Salix association and remained very wet throughout the season. Yellow water lilies (Nuphar variegatum Engelm.) grew in the open water which was bordered abruptly by tall, thick Carex rostrata and Menyanthes trifoliata. Further inland the Carex was shorter and grew in association with young Salix and the mosses, Drepanocladus revolvans var. intermedius (Lindb.) and D. vernicosus (Lindb.), interspersed with small Populus tremuloides and Eriophorum angustifolium, with a few Triglochin maritima, Menyanthes trifoliata, Juncus sp. and Equisetum spp. Algal growth was quite thick by the beginning of July. Sampling was carried out in the zone of emergent vegetation on the north-west side of the lake. A small stream flows slowly from the north end of the lake to the Pembina river.

Gammarids were abundant for the duration of the summer and a few Cladocera were regularly taken in samples after the first week of

June. Trichoptera (Limnephilus sp.), which were very common in May, decreased markedly in numbers during June and July, but became common again at the end of July. A succession of Zygoptera (Enallagma sp., Nehalennia irene and Lestes congener Hagen) maintained large numbers of this group for the whole season, whilst small Anisoptera were common in June (Leucorrhinia hudsonica) and in late July (Aeshna eremita). Chironomid larvae were common from the end of May onwards, and a few pupae were taken each week from early June to late July. A few Ceratopogonids were present in May and June, but mosquito larvae were rare. Coleoptera larvae (Graphoderus sp. and Dytiscus sp.) were common during June but declined in July, and adults, although earlier to appear, were fewer in numbers. Ephemeroptera larvae (Siphonurus sp.) appeared at the end of May and were common in June; the population fell in July but larvae were found again at the beginning of August. Notonecta spp. were very common in June and July, whilst Corixa sp. was less common but present through the whole season. Molluscs (Planorbis sp.) were common in May.

Ten species of dragonfly larvae were collected from Scaup Lake. Aeshna eremita and Leucorrhinia hudsonica were the commonest forms, but Aeshna canadensis, Leucorrhinia proxima Calvert and Cordulia shurtleffi Scudder from this habitat, figured prominently in the analyses.



a) The Roadside Ditch, Flatbush, looking west. July 1962.



b) Watt's Pond, Flatbush, looking south-west. The sampling area is in the foreground. July 1962.



a) The sampling station at Lake Sara, Flatbush, before the new growth of emergent vegetation had appeared above the water . May 1962 .



b) Scaup Lake, Flatbush, looking south from the sampling area. July 1962 .



a) Proel's Marsh, Flatbush, looking north-west. A thick growth of sedge obscures the water surface. July 1962.



b) Totem Pond, near Edmonton. July 1961.



a) The sampling station at Winterburn Swamp, near Edmonton. August 1961.



b) A path in the bush at Flatbush; a favourite haunt of many of the smaller adult Libellulids. July 1962.

e. Proel's Marsh (Plate 5)

This was a marshy area, 80 m. x 40m., and completely covered and dominated by Carex rostrata, interspersed with Salix bushes, Eriophorum angustifolium, Equisetum limosum and E. arvense. Carex aquatilis Wahlenb. and Calamagrostis canadensis were common around the edges. The marsh was bordered by tall aspen poplar trees on the north, west, and south sides, but the east side had only a few small aspen and Salix bushes, and from these a grassy bank ran up to the road. The bottom was soft, consisting mainly of dead Carex and other vegetable matter. The sampling area occupied a band, three metres wide, by the bank on the east side.

Mosquito larvae (Culex territans) were common in June and Anopheles earlei appeared in low density in mid-July and August. Chironomid larvae were common for the whole season and a few pupae were present in June and early July. Chaoborus sp. larvae and Ceratopogonid larvae were rare. Coleoptera larvae (Graphoderus sp., Hydaticus sp. and Dytiscus sp.) and adults were both common for the whole summer. A few Corixa sp. were taken regularly after mid-June, but Notonecta spp. were rare. There were no Gammarids, but small Crustacea (mainly Cladocera) were very common, and Molluscs (Limnea sp. and Planorbis sp.) were also commonly found at all times. Ephemeroptera were rare and Trichoptera larvae (Phryganea sp.) were found only in August. There were few Zygoptera during the first half

of the season, but Coenagrion resolutum was common in August.

Aeshnids were rare in this habitat and the dragonfly larva fauna consisted almost entirely of Leucorrhinia hudsonica.

5.32 Habitats in the Edmonton area

This area lies in the parkland country, which is characterized by fairly open country with stands of aspen poplar (Populus tremuloides). Specimens were collected from three habitats at various times during the summer of 1961.

f. Devon Pond

Specimens were collected from this pond in May. It was situated ten miles west and ten miles south of Edmonton on Alberta Highway 60, and lay in a soft spongy area dominated by Sphagnum moss. Emergent vegetation (Carex sp., Calamagrostis canadensis, Calla palustris and Typha latifolia) bordered the pond, which was then surrounded by swamp birch bush (Betula pumila glandulifera).

During May, small Ostracods were very abundant and Zygoptera and Trichoptera were common. Chironomid larvae and Gammarids were few, as were Corixids and Coleoptera larvae.

Collection of Anisoptera larvae was made somewhat difficult by the very soft terrain. Leucorrhinia borealis Hagen was the commonest species and most of the population emerged synchronously

during the fourth week of May. Specimens of Aeshna interrupta lineata were also collected and used in the analyses.

g. Totem Pond (Plate 5)

This was a small pond eight miles west of Edmonton on Alberta Highway 16. It was surrounded by Salix sp. and Populus tremuloides bushes below which, thick, tall Agropyron sp. extended up to the water's edge. The emergent vegetation was well developed and consisted mainly of Carex rostrata, with Typha latifolia and some Calamagrostis canadensis. Lemna sp. was common and accumulated on the east side of the pond. The bottom was muddy with a certain amount of dead vegetation, but it was firm and the water was clear.

Trichoptera (Limnephilus sp. and Phryganea sp.), Ephemeroptera (Siphonurus sp. and Chloëon sp.) and Zygoptera (Coenagrion resolutum, Enallagma sp.) were all present in large numbers at the times when the collections were made, and Coleoptera larvae (Hydrophilus sp. and Dytiscus sp.) were even commoner. Corixa sp. was very common in September and so were Chaoborus sp. larvae. Chironomids were not present in particularly high numbers and there were no Culicine larvae. There were no Gammarids, but Ostracods were present in large numbers, and Molluscs (Limnea sp., Physa sp., and Planorbis sp.) were common in later samples.

Larvae of Aeshna interrupta lineata and Sympetrum danae

Sulzer were collected from the emergent vegetation zone in May and June and again in September.

h. Winterburn Swamp (Plate 6)

Larvae were collected from two sloughs in this large swampy area during August. Sphagnum moss was dominant and emergent vegetation was restricted to small amounts of Carex sp., Calamagrostis canadensis and Juncus sp. The bottom was composed of flocculent, decayed Sphagnum to a great depth. Thick stands of spruce and larch surrounded the sloughs.

Chironomid larvae were very common and Coleoptera larvae, although few in numbers, were found in all samples. A few Ephemeroptera and Chaoborine larvae were taken in early samples and Zygoptera larvae were common at this time. Small Crustacea were common but there were no Gammarids and no Trichoptera larvae, and Corixa sp. was rare.

5.4 Laboratory observations as a guide to the types of food eaten in nature

Dragonfly larvae will eat a wide range of animals in the laboratory (Table 1), and although such observations tell us little about the food in nature, these animals could form a part of the natural diet should they occur together with dragonfly larvae. Such animals range from slow moving Gastropods to fast moving Gammarids, and from

small, compact Ostracods to long, thin Zygoptera and even individuals of the same species and size as the predator itself.

Although there may be little selection of prey that is to be caught, not all prey that is clasped by the dragonfly's labial palps is eaten; certain forms are repeatedly rejected. For example, larvae of Leucorrhinia proxima (17-18 mm. in length) have been seen to catch but release Haliplid adults (2.5 mm.), Dytiscid adults (2-4 mm.), and Hydracarina (1-2 mm. in diameter). Similarly, many species always rejected plant material such as floating pieces of vegetation, and non-living objects such as paper dummies. Warren (1915) has noted that many ants, especially those rich in formic acid, and the black and orange aphid Myzus citricidus Kirk, were struck at repeatedly by Anax and Pantala larvae but were often rejected.

From these observations it may be postulated that, first, the food must be living and must be animal in nature. And second it must be soft enough and must not be distasteful. The chemical selection of food is considered further in Section 4, along with the sensilla that are thought to be important in receiving gustatory stimuli. Although there are few distasteful animals that are likely to be captured by dragonfly larvae in their natural environment, the rejection of captures that cannot be broken by the mandibles, particularly adult beetles, is common.

TABLE 1. - Examples of food eaten by dragonfly larvae in the laboratory

The figures in parentheses are lengths in millimetres.

Prey	Predator
<u>Chaoborus</u> sp. larvae (8)	<u>A. interrupta</u> (32) <u>L. quadrimaculata</u> (22)
Chironomid larvae (4)	<u>L. quadrimaculata</u> (22)
Culicine larvae (4-7)	<u>A. interrupta</u> (30, 15) <u>L. hudsonica</u> (15) <u>L. quadrimaculata</u> (22) <u>S. danae</u> (15)
Coleoptera larvae (8)	<u>A. interrupta</u> (32) <u>L. quadrimaculata</u> (22)
Corixid adults (7)	<u>A. canadensis</u> (26) <u>A. interrupta</u> (35) <u>L. borealis</u> (22)
Ephemeroptera larvae (11)	<u>A. interrupta</u> (18) <u>L. quadrimaculata</u> (22)
Trichoptera larvae (10-17)	<u>A. eremita</u> (30) <u>A. interrupta</u> (30) <u>L. borealis</u> (21)
Anisoptera of same species and size	<u>A. interrupta</u> (14, 30) <u>L. hudsonica</u> (14) <u>S. danae</u> (15)
Zygoptera larvae (15-19)	<u>A. canadensis</u> (27) <u>A. interrupta</u> (35) <u>L. quadrimaculata</u> (25) <u>L. hudsonica</u> (16)
Cladocera (1)	<u>A. interrupta</u> (30) <u>L. proxima</u> (18)

TABLE 1. - cont'd

Prey	Predator
Gammaridae (3-6)	<u>A. canadensis</u> (23) <u>A. interrupta</u> (34) <u>L. quadrimaculata</u> (23) <u>L. hudsonica</u> (15)
<u>Limnea</u> sp. (8)	<u>A. interrupta</u> (36)
<u>Planorbis</u> sp. (3)	<u>A. interrupta</u> (38) <u>L. quadrimaculata</u> (22)
Oligochaeta (25)	<u>L. quadrimaculata</u> (22)
Hirudinea (25)	<u>A. interrupta</u> (27)
<u>Simulium</u> sp. adult (3)	<u>A. eremita</u> (35)
<u>Aedes</u> sp. adult (6)	<u>L. hudsonica</u> (15)
Various kinds of fish	<u>Anax</u> and <u>Pantala</u> *
Protozoa, Rotifera, and Nematoda	<u>Anax</u> and <u>Pantala</u> *
Several orders and families of terrestrial insects	<u>Anax</u> and <u>Pantala</u> *

* Warren (1915)

These laboratory observations help to explain the absence of certain forms from the diet in nature, but the composition of this diet also depends on a complex of factors including the abundance and distribution of prey animals in a particular habitat, their size ranges, and the ease with which they are caught. These factors are examined in the following two sections.

5.5 The prey of dragonfly larvae in nature

Chaoborine larvae formed only a small part of the food of dragonfly larvae in the habitats studied, mainly because their distribution did not correspond with that of the predators. They were common at times in the Roadside Ditch, Totem Pond and Winterburn Swamp but were absent or rare at the other habitats. However, when they did occur together with dragonfly larvae they were eaten, and at the Roadside Ditch 16 per cent of the dragonfly population had taken them. Only Aeshnids, especially Aeshna interrupta lineata, and a few Sympetrums preyed on Chaoborine larvae. These prey animals are not easily seen when stationary or moving slowly, but when they move jerkily they are probably very attractive to dragonfly larvae (see Section 7.42). Although the predators may temporarily 'lose' their prey in between jerks this is not thought to be an important factor as dragonfly larvae are still attracted to slow movements of the prey after they have been stimulated by more rapid phases.

Chironomid larvae were the commonest item in the diet of dragonfly larvae in nature. So many are eaten that despite their small size they probably make up the greater part of the food. They were common in all habitats except Devon Pond and Totem Pond and in all except these two they were eaten by a larger proportion of dragonfly larvae than was any other single item of prey. Apart from their abundance, Chironomid larvae have several characters that make them acceptable to dragonfly larvae. They are conspicuous by their wriggling motion, they are easy to catch being of convenient size and lacking protective devices such as speed of movement, and they are soft and quite small and so can be eaten quickly. That relatively few dragonfly larvae ate Chironomid larvae in Devon Pond and Totem Pond emphasizes the importance of local abundance as a factor in prey selection. Although Chironomid larvae were eaten by all sizes of dragonfly larvae, the smaller individuals (under 20 mm.) preyed on them more.

Chironomid pupae are not easily accessible to dragonfly larvae. They occur only for a short time and remain inactive at the surface. But whenever they occurred in the same habitats as dragonfly larvae a few were eaten by Aeshnids and climbing Libellulids, but bottom-living forms such as Libellula quadrimaculata and Cordulia shurtleffi did not take them.

Ceratopogonid larvae are small and very thin but their snake-like method of swimming probably makes them conspicuous to dragonfly

larvae. Nowhere were these prey animals very common and they seldom occurred in faecal pellets, but they inhabited all levels and were eaten by most forms from sprawlers to climbers.

The habits of mosquito larvae make them most susceptible to attack by dragonfly larvae. However, they rarely occurred in the same habitats since, in this area, dragonfly larvae require permanent waters whilst most mosquito larvae are found in temporary pools. Culex territans and Anopheles earlei do, however, inhabit more or less permanent waters and these two species were found in Watt's Pond and in Proel's Marsh, where, over the whole season, they were eaten by 10 and 15 per cent of the dragonfly population respectively. In June and August, when these two mosquito species were most common, 18 per cent of the dragonfly larvae collected from Watt's Pond and Proel's Marsh had the remains of mosquito larvae in their faecal pellets.

Beetle larvae were common in all habitats except Devon Pond and Winterburn Swamp. The full grown larvae of Dytiscus were not attacked but earlier instars of this and other smaller beetle larvae formed a significant part of the diet of most species of dragonfly larvae. Beetle larvae have a slow and somewhat awkward locomotion and they are probably easily seen and caught by dragonfly larvae.

Adult beetles were common everywhere but formed only a small part of the food of dragonfly larvae. They are struck at, but

because of their hard, shiny cuticle they are difficult to hold and difficult to chew. Aeshnids have more trouble holding adult Coleoptera than do Libellulids in which the cage-like mask is fitted for trapping such prey, and most of the adult beetles that were eaten had fallen prey to Libellulids. I have no evidence that dragonfly larvae learn not to strike at these prey animals which they cannot chew.

Corixids are active insects in both larval and adult stages and although activity attracts the attention of dragonfly larvae, they have difficulty getting within striking distance and effecting the capture. Frost and Macan (1948) and Ball (1961) have observed that certain species of fish do not eat Corixids in proportion to their abundance, possibly because these bugs secrete a distasteful substance. In the laboratory, dragonfly larvae that captured Corixids seldom ate the whole animals, and it seems likely that these prey animals are also distasteful to dragonfly larvae. At any rate, records of dragonfly larvae having eaten Corixids are few, even though they were quite common in several habitats.

Mayfly larvae may be somewhat protected by a vigorous escape reaction when attacked, but they were eaten by both climbing and sprawling dragonfly larvae and they formed a significant part of the food at times when they were common. Local abundance was again an important factor, larger numbers of dragonfly larvae having taken this prey in the Roadside Ditch, Scaup Lake, and Totem Pond, where it was common.

Trichoptera larvae, although generally slow moving, do jerk their heads and wave their legs as they search for supports or add material to their cases, and this movement attracts dragonfly larvae. When captured, a caddisfly larva attempts to retract into its case but it is generally prevented from doing so by the strong hold of the dragonfly's labial palps. Trichoptera larvae were eaten mainly by Aeshnids whose sharp labial palps are better suited for holding the captive prey and preventing it from retracting completely into its case, than are the non-piercing palps of the Libellulids. Limnephilid larvae are climbers like the Aeshnids, the Leucorrhinias and the Sympetrums, which all fed on this prey. There are no records of bottom-living dragonfly larvae having eaten Limnephilids.

Other Anisoptera form a very small part of the diet of dragonfly larvae in nature. In the laboratory, dragonfly larvae will only attack individuals of their own kind and size when they are very hungry, and this situation is not likely to occur in nature where more convenient food is usually abundant. But there is no reason why they should not prey on smaller dragonflies of any species should they come into contact, although small individuals may have a different distribution from that of larger individuals (Corbet, 1957), and furthermore, the banded or mottled colouration of small Aeshnid larvae may serve as camouflage and protect them from larger Anisoptera. Apart from single records at Watt's Pond and Winterburn Swamp, the only place

where Anisoptera were eaten was at Scaup Lake, where a large population of small Leucorrhinia hudsonica appeared in June and was preyed upon by larger Aeshnids.

Zygoptera larvae formed a large part of the food of all dragonfly larvae in all habitats. As they move slowly amongst vegetation they fall easy prey to Anisoptera in ambush, and Aeshnids especially fed on them extensively.

The jerky movement of small Crustacea, such as Cladocera and Ostracoda, is a good stimulus for the release of the strike by the dragonfly, and these small animals appeared in the food in numbers that were related to their abundance in the habitat. In Devon Pond, where Ostracods were particularly abundant, over 70 per cent of the faecal pellets from dragonfly larvae contained their remains. It is a mark of the accuracy of Aeshnid larvae that they can catch such small prey with their broad, flat labia. That the cage-like masks of Libellulids and Corduliids are much better fitted for this task is reflected in the analysis of faecal pellets.

Gammaridae are difficult to catch on account of their high speed and their hard, shiny cuticle. In the laboratory (Section 7.3), they were missed more often than not, but in places where they were abundant they did make a significant contribution to the food of dragonfly larvae in nature. In Scaup Lake, Gammarids were very

common throughout the year and they appeared in 24 per cent of the faecal pellets examined, but in Watt's Pond, Lake Sara, and Devon Pond, where they were less common, only 1-5 per cent of the dragonfly population had eaten them, stressing once again the importance of local abundance.

Large water mites have a very hard cuticle and they cannot be chewed easily by dragonfly larvae; they are usually rejected (Section 5.4). All Hydracarina that figured in the present study were very small and had been ingested whole, and it seems likely that they were not struck at, but eaten accidentally whilst they were attached to larger items of the dragonfly's diet.

Small Molluscs were eaten in numbers proportional to their abundance wherever they occurred. They had very thin shells and small forms were eaten whole, but undoubtedly only the soft parts of larger forms were eaten and no remains of these showed up in the faecal pellets.

Aerial insects such as Thysanoptera, small Hymenoptera and small Diptera may become trapped by surface tension at the water surface and are then available to dragonfly larvae as prey. Only larvae that climb in vegetation near to the surface will see and be in a position to take advantage of this source of food.

Small fish were absent from all habitats except Lake Sara, and

here they were rare and no fish scales appeared in faecal pellets of dragonfly larvae from this habitat.

Mud-dwelling Oligochaete worms and leeches were common in most of the habitats and both were almost certainly eaten by dragonfly larvae. It was impossible, however, to obtain an estimate of the contribution made by these forms to the food of dragonflies because of the lack of hard parts.

Notonectids were common as larvae and as adults in several habitats but did not appear in the faecal pellets of dragonfly larvae. They are large, active insects and are also quite hard, and these factors make them difficult to catch, hold and consume.

5.6 Discussion

Dragonfly larvae are general animal feeders and will strike at any moving prey that is below a certain size. Very small prey and fast-moving forms are often missed, and prey with a vigorous escape reaction may break away from the labial palps of its captor, whilst hard forms will not yield to the predator's mandibles and will be rejected. With these exceptions, however, a dragonfly larva feeds on most animals in proportion to their relative numbers in the environment as is shown in Figure 30. Particularly clear examples are: the presence of Chaoborine larvae in the Roadside Ditch; the few Chironomid

larvae in Devon Pond and Totem Pond; more Ceratopogonids in Lake Sara then in the other habitats; Culicine larvae in Watt's Pond and Proel's Marsh; the larger numbers of Coleoptera larvae in the Roadside Ditch and Totem Pond; more Ephemeroptera in the Roadside Ditch, Scaup Lake, and Totem Pond than in the other habitats; more Trichoptera in the Roadside Ditch, Scaup Lake, Devon Pond, and Totem Pond; small Anisoptera occurring abundantly in Scaup Lake; small Crustacea in Proel's Marsh and Devon Pond; Gammarids in Scaup Lake; and Molluscs in Lake Sara.

We may thus expect seasonal changes to occur in the food in direct relation to changes in the relative abundance of different groups of prey. This is difficult to show without taking large samples of all prey animals over a longer period of time, but observations on the sudden appearance of groups of prey and estimates of their abundance were often correlated with the composition of remains in faecal pellets. Certain groups from various habitats have been selected to show this facet of the feeding of dragonfly larvae in nature, and the fluctuations of these animals in the food are shown in Figure 34.

Chironomid larvae (Figure 34a) were not rare at any time at Scaup Lake, but they did become commoner in June, reached a peak in mid-July and underwent a decrease in numbers in August. This general trend was similar to that shown by the frequency of Chironomid remains in faecal pellets.

Large numbers of small Leucorrhinia hudsonica were present in Scaup Lake in June and small Aeshna eremita were abundant in July (Figure 34b). Anisopteran remains appeared in the faecal pellets from mid-June to the beginning of August.

Ephemeroptera larvae (Figure 34c) appeared rather suddenly in Scaup Lake at the beginning of June, and at the same time appeared in faecal pellets. Their numbers in both the habitat and faecal pellets declined during July but increased again in August.

Coleoptera larvae (Figure 34d) did not appear in any numbers in the sampling area at Scaup Lake until the end of May and simultaneously they were recorded from faecal pellets. They were common in June but their numbers declined in July.

Further examples come from other habitats. There was a correlation between the appearance of Culicine remains (Figure 34e) in faecal pellets collected from Watt's Pond in mid-June and early August, with peaks of Culex territans and Anopheles earlei abundance at these times.

In Lake Sara, Molluscs (Figure 34f) were common in early May, rare through late May and June, and then very common in July, and they had a similar distribution in faecal pellets from dragonfly larvae in that habitat.

Chironomid larvae (Figure 34g) were present in Watt's Pond throughout the season, but were relatively few until the middle of June. After this they steadily increased in numbers both in the environment and in the food of dragonfly larvae.

At Proel's Marsh, Zygoptera (Figure 34h) were very few until August, when they became common, and it was not until this time that they were preyed on extensively by dragonfly larvae.

Also at Proel's Marsh there were two peaks in the mosquito larva population (Figure 34i); the first was in June and the second in early August, and these prey animals formed an important part of the food of dragonfly larvae at these times.

As a final example, we may take Chaborine larvae (Figure 34j) which appeared in the Roadside Ditch in the first week of August. At the same time they were recorded from faecal pellets and they were common in the habitat and in the food of dragonfly larvae in the second week in August.

But the abundance of each group as a whole is not always sufficient evidence for predicting the composition of the food of dragonfly larvae in nature. The abundance of other groups of animals will affect the extent to which a particular group is preyed upon. This latter argument may apply to the part played by Gammarids in the food of dragonfly larvae at Scaup Lake in early May. Although their numbers did not decrease appreciably during May, there was a

pronounced drop in the frequency with which they appeared in faecal pellets. This may have been associated with the appearance and increase in abundance of other groups that were easier to catch than Gammarids.

The relative sizes of predator and prey are always important and certain kinds of prey, although they may be abundant, may not be available to the smaller size-groups of dragonfly larvae on this account. An example of this occurred in several habitats in mid-July, when small Leucorrhinia hudsonica (5-10 mm. in length) were common. At this time, final instar Zygoptera larvae were also common and they formed an important part of the food of larger dragonfly larvae, but they were not eaten by the small Leucorrhinia hudsonica which fed almost exclusively on Chironomids.

Certain groups of prey animals such as Chironomid larvae are generally not denied to any but the very smallest dragonfly larvae on account of size alone. Their abundance and accessibility relative to other groups are then the important factors governing their selection as prey. Animals which may reach quite a large size will also be eaten consistently if they develop at such a time and rate that the predator has a distinct size advantage at all times. It is when life cycles are out of phase, as with Leucorrhinia hudsonica and Zygoptera, that size differences exert their effect. The changing size compositions of all populations would be needed to determine just how much effect this matter of synchronization of the life cycles has on the food taken by different sized larvae. At the moment it seems that the overall

distribution of size-groups is such, that the various groups of prey animals are present in much the same proportions in the food of all size-groups of dragonfly larvae except the very smallest (Figures 32 and 33).

These examples demonstrate the advantages of a general feeding system. The choice of prey is wide and should the availability of a single item be reduced through reason of its size or its scarceness, this void will be filled by other groups, even to the extent of cannibalism. In the places where dragonfly larvae live, there is usually a sufficiency of suitable prey and food is never likely to have a limiting effect on the survival of the population. The amount of food in different microhabitats may, however, affect the speed of development of larvae living there (Corbet, 1962).

There are few differences in the compositions of the food of the different species of dragonfly larvae in a single habitat. Bottom-living forms such as Libellula quadrimaculata and Cordulia shurtleffi, do not eat prey such as Chironomid pupae and aerial insects, which are found only at the surface and are more accessible to climbing forms such as species of Aeshna, Leucorrhinia, and Sympetrum. Aeshnids eat more of those prey animals that often grow to large size such as Trichoptera, Ephemeroptera, and Zygoptera larvae, than do the smaller Libellulids. The large size to which Aeshna larvae grow and the arrangement of their life cycles, leads to a situation whereby they enjoy a size advantage with respect to this type of prey more

often than do Libellulids. Libellulid and Corduliid larvae have a type of labium (see Section 2.1) that is better fitted for holding small, elusive prey, than is the labium of an Aeshnid, and such prey as Cladocera, Ostracoda and Gammarids do figure more prominently in the food of the former group. Certain results in Figure 31 may be misleading in that they reflect the abundance of the prey in a particular habitat rather than a selection on the part of the predator. For example, most Leucorrhinia borealis were collected from Devon Pond where Ostracods were abundant and Chironomids rare; most Libellula quadrimaculata were collected from Lake Sara at a time when Molluscs were common; and most Cordulia shurtleffi were collected from Scaup Lake where Gammarids were particularly common. Such results, however, do serve to emphasize the importance of local abundance of prey animals as a factor governing the composition of the food of dragonfly larvae in nature.

Dragonfly larvae collected at different times during daylight hours have always had food in their guts. They do not feed continuously and may show a daily rhythm like many other animal activities. But it would be difficult to relate the intensity of their feeding to an endogenous rhythm, since it probably depends on the activities of their prey.

In the laboratory, with abundant food close at hand, dragonfly larvae often feed voraciously until they are satiated, and faecal pellets

are usually voided overnight no matter what time of day feeding occurred. But larvae collected in the field usually contain only three, or less, prey animals. If faecal pellets are voided only at night, as in the laboratory, then we would expect larvae collected in the evening to contain a whole day's food in their guts. From this, it would appear that dragonfly larvae are not as voracious in nature as they are usually considered to be, and this hypothesis is further supported by the observation that, excluding forms that appeared to be nearing metamorphosis, 11 per cent of 1015 larvae collected had empty guts. The range was from 0.9 per cent for Sympetrum spp. to 30 per cent for Leucorrhinia borealis, although this high figure for the latter may have included some forms that were nearing emergence. Larvae will take any food that becomes available and if it is very abundant and at close range they will feed greedily. But in nature dragonfly larvae are seldom immediately surrounded by an abundance of prey and they are content to wait in ambush for the prey animals that will come their way. If food becomes scarce they can endure long periods without it (Tillyard, 1910).

In summary, it may be said that dragonfly larvae are general animal feeders and will attack a wide range of animal life. The composition of the food of dragonfly larvae in nature is affected by a complex of factors including the relative abundance of different prey in the environment, the size and habits of this prey and the ease with which it is caught and devoured. Similar factors are important in the

selection of prey by various species of carnivorous fish (Ball, 1961; Corbet, 1961).

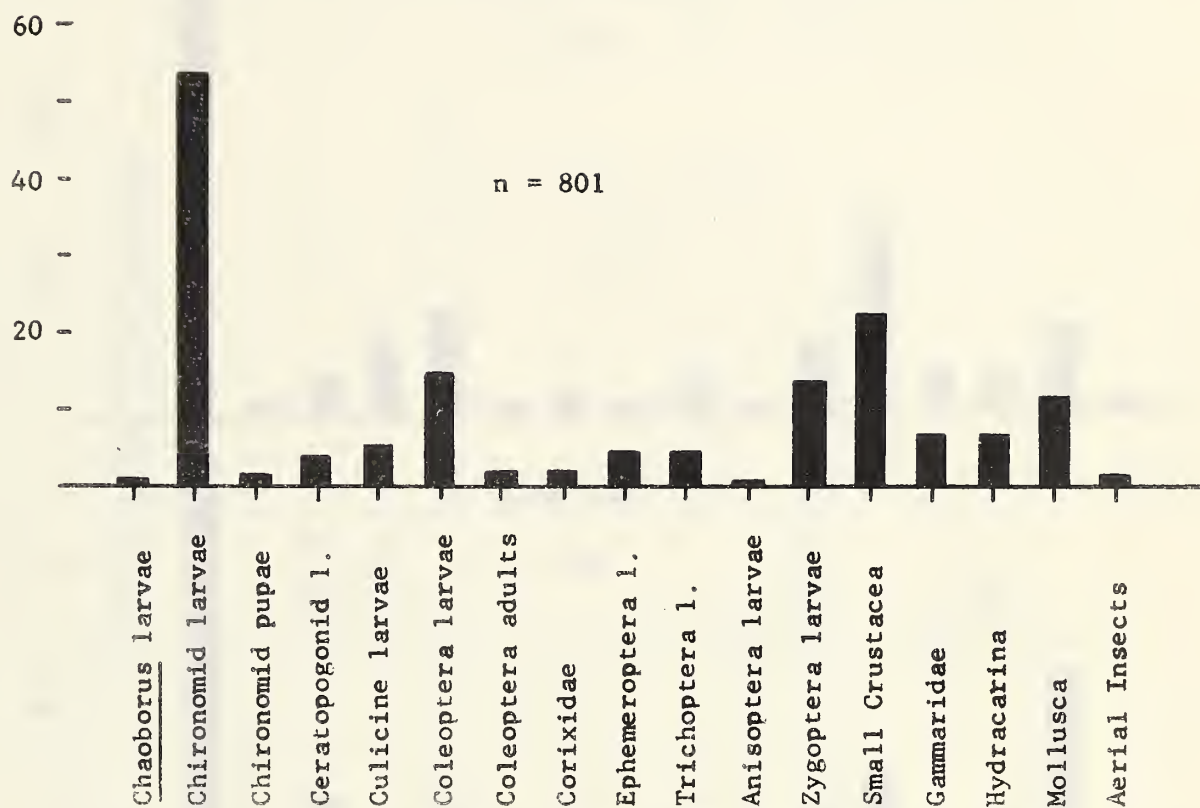


FIG. 29. - The prey of all dragonfly larvae from all habitats. The number of dragonfly larvae in which each type of prey occurs is expressed as a percentage of the total sample.

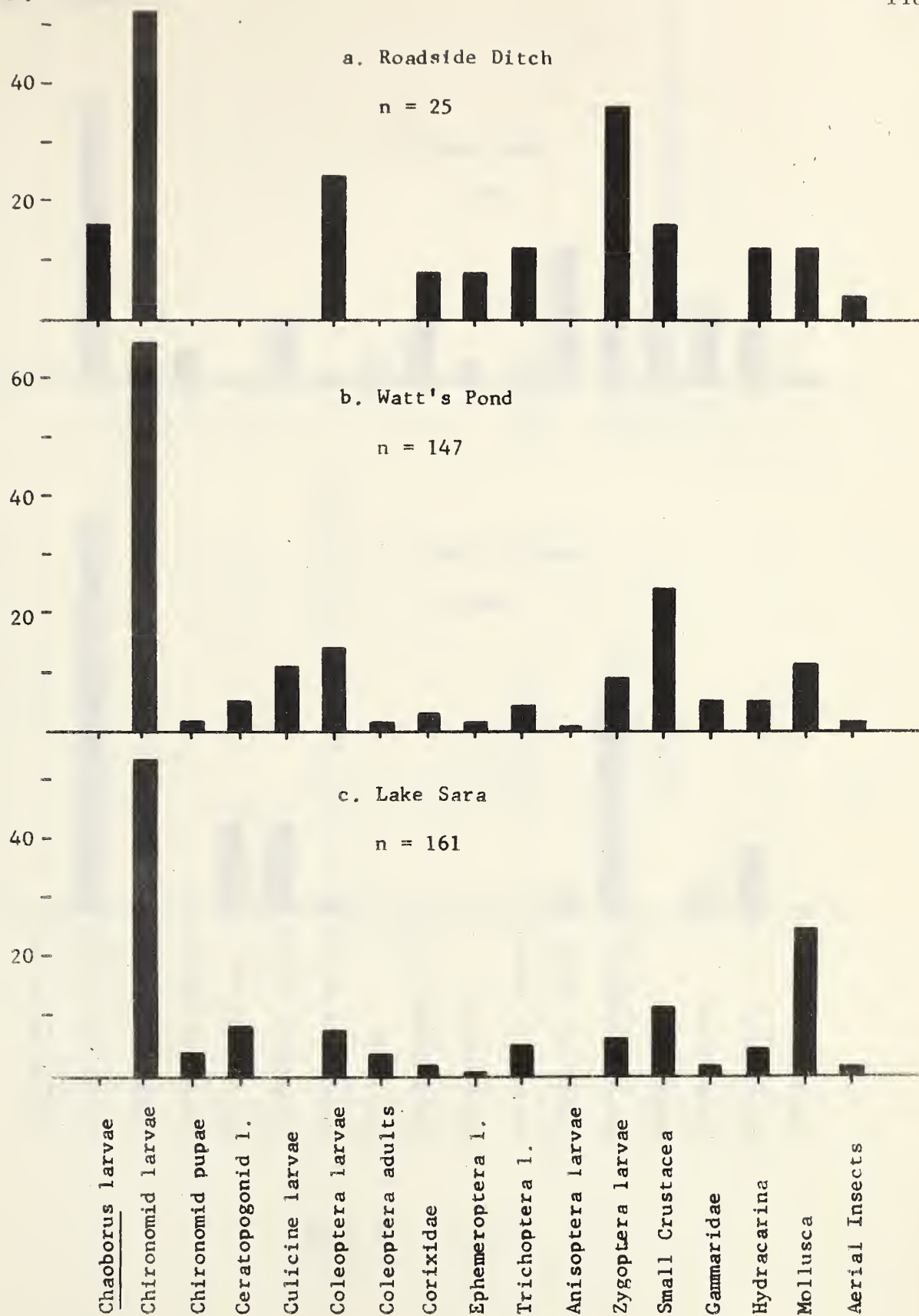


FIG. 30. - The prey of dragonfly larvae from different habitats.
Units as in FIG. 29.

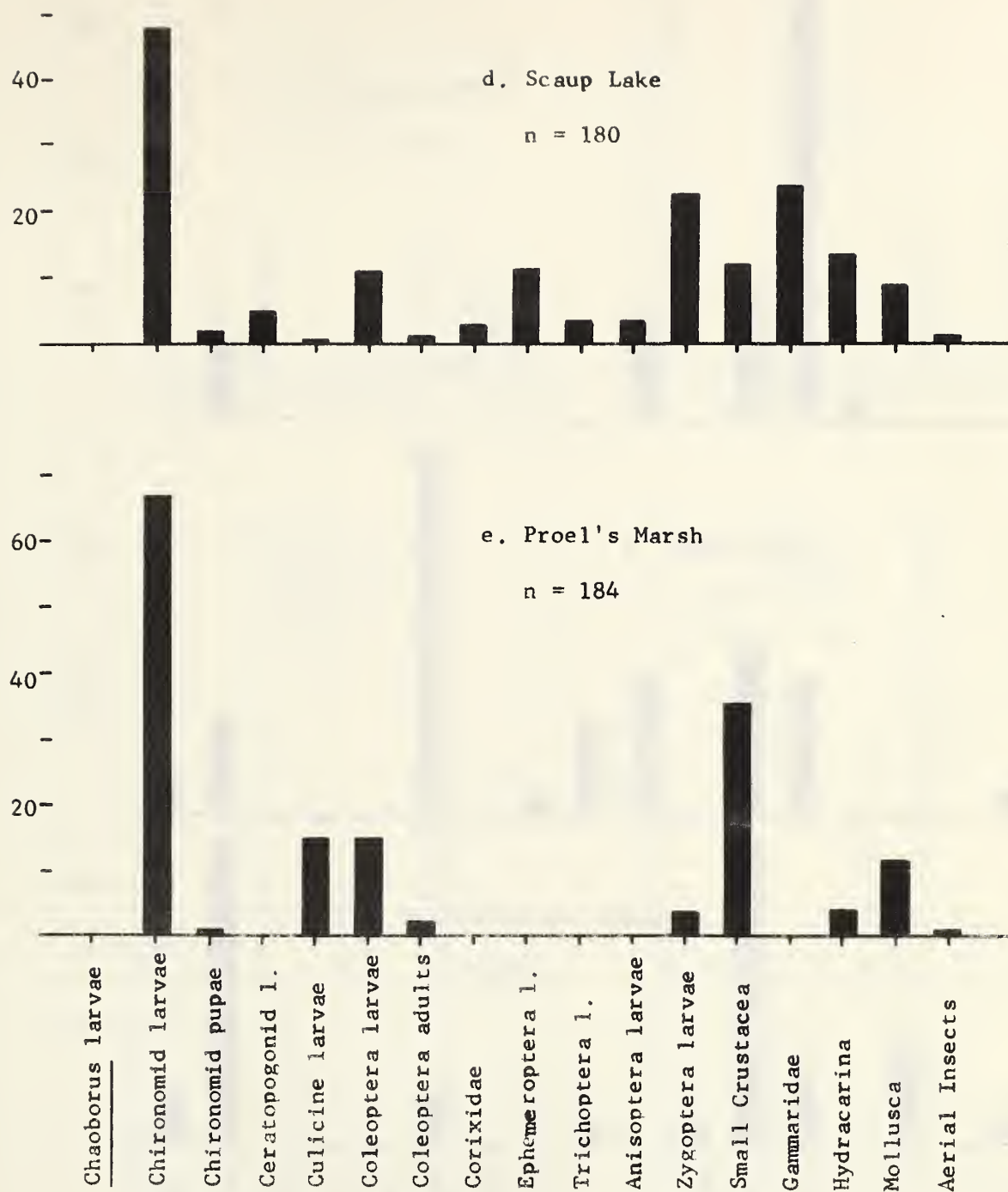


FIG. 30. - cont'd.

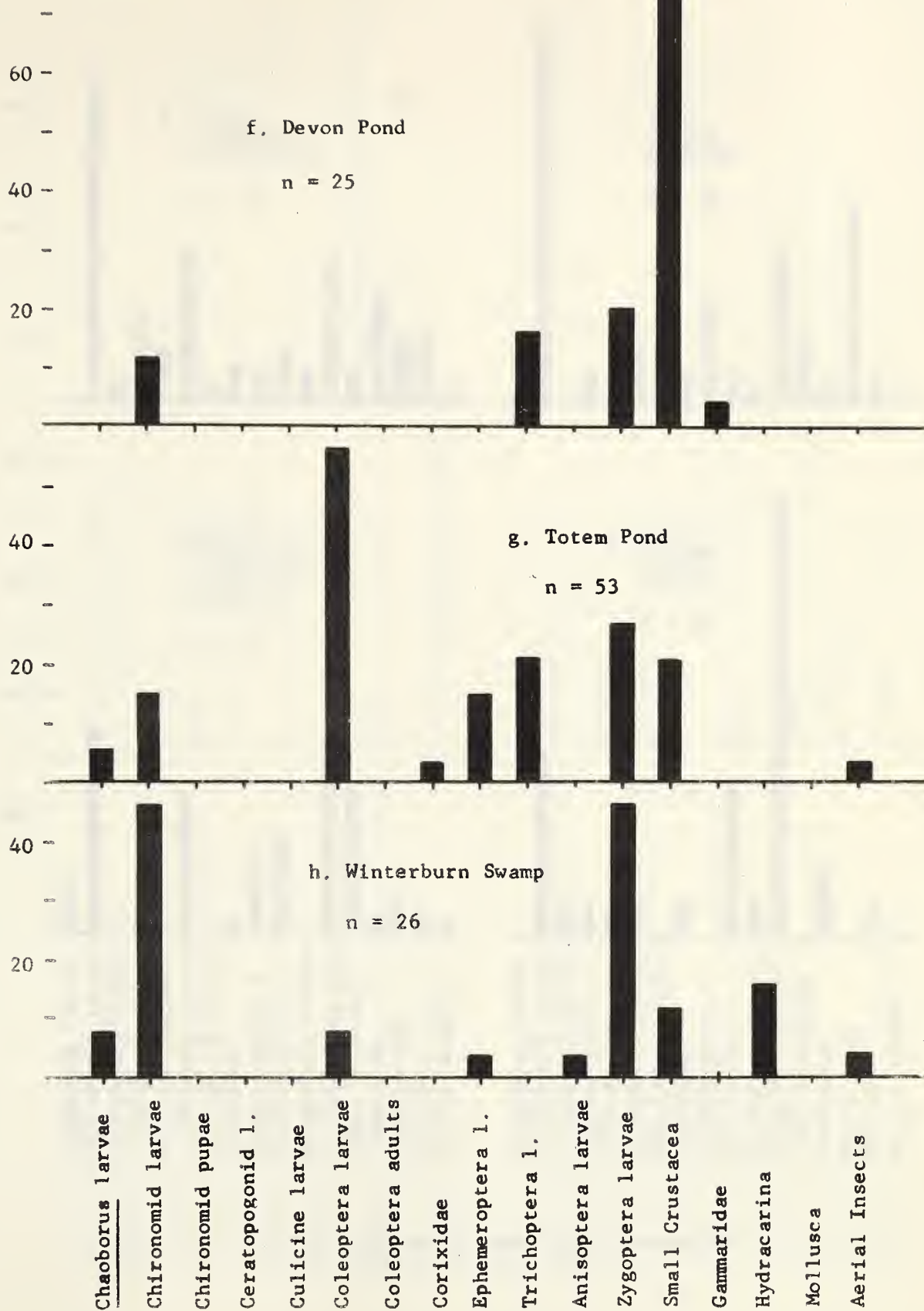


FIG. 30. - cont'd.

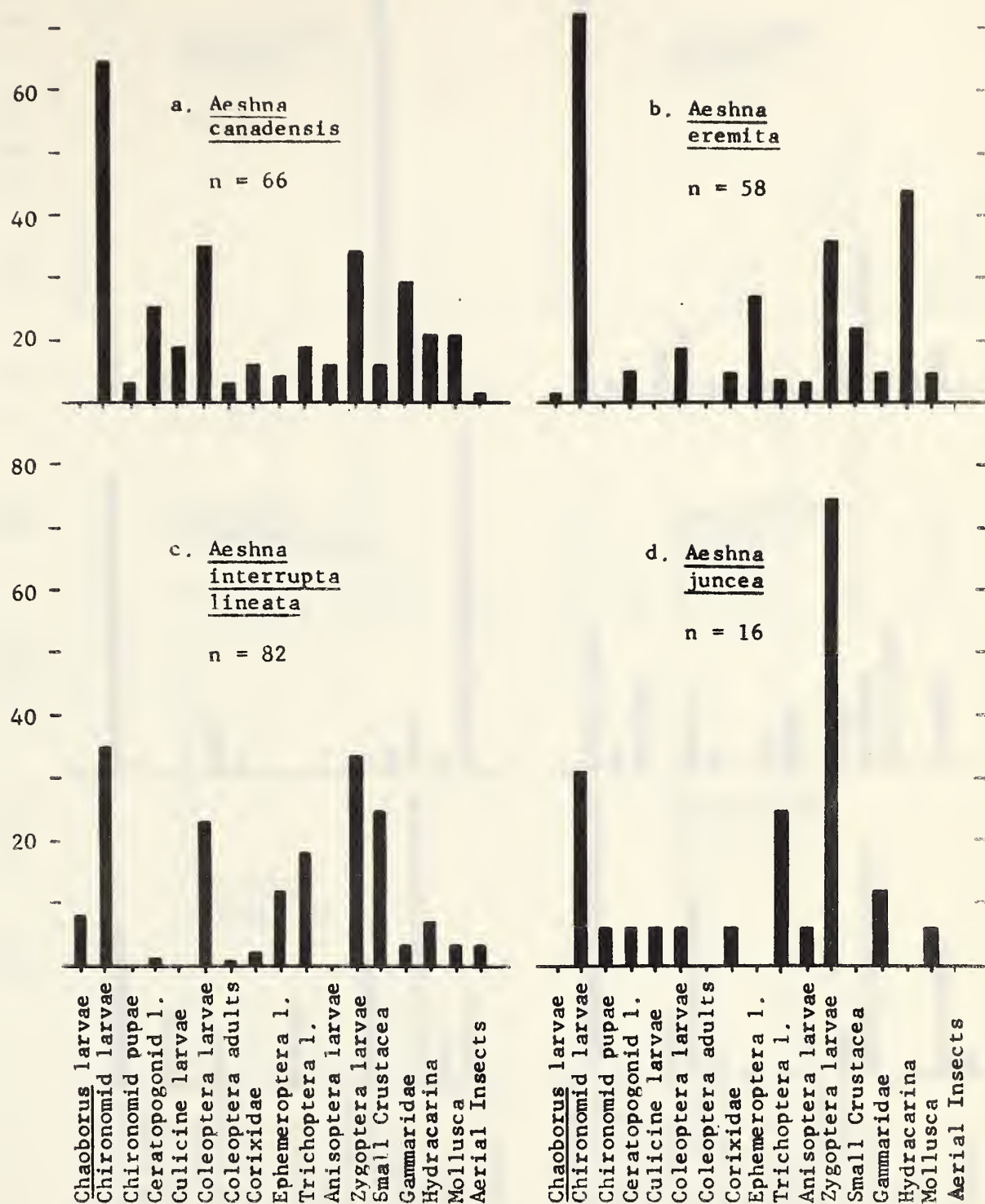


FIG. 31. - The prey of certain species of dragonfly larvae.
Units as in FIG. 29.



FIG. 31. - cont'd.

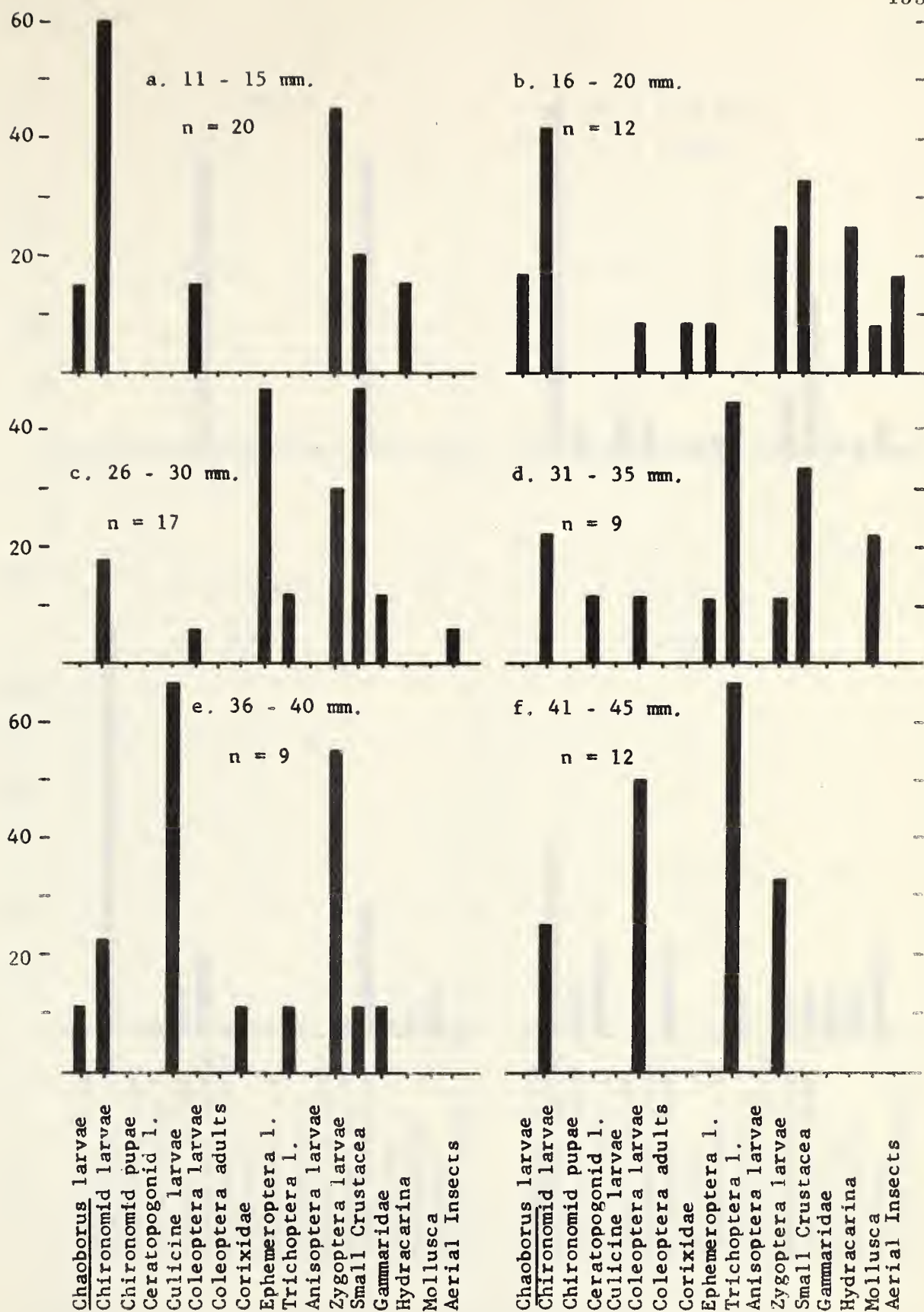


FIG. 32. - The prey of certain size-groups of *Aeshna interrupta lineata*. Units as in FIG. 29.

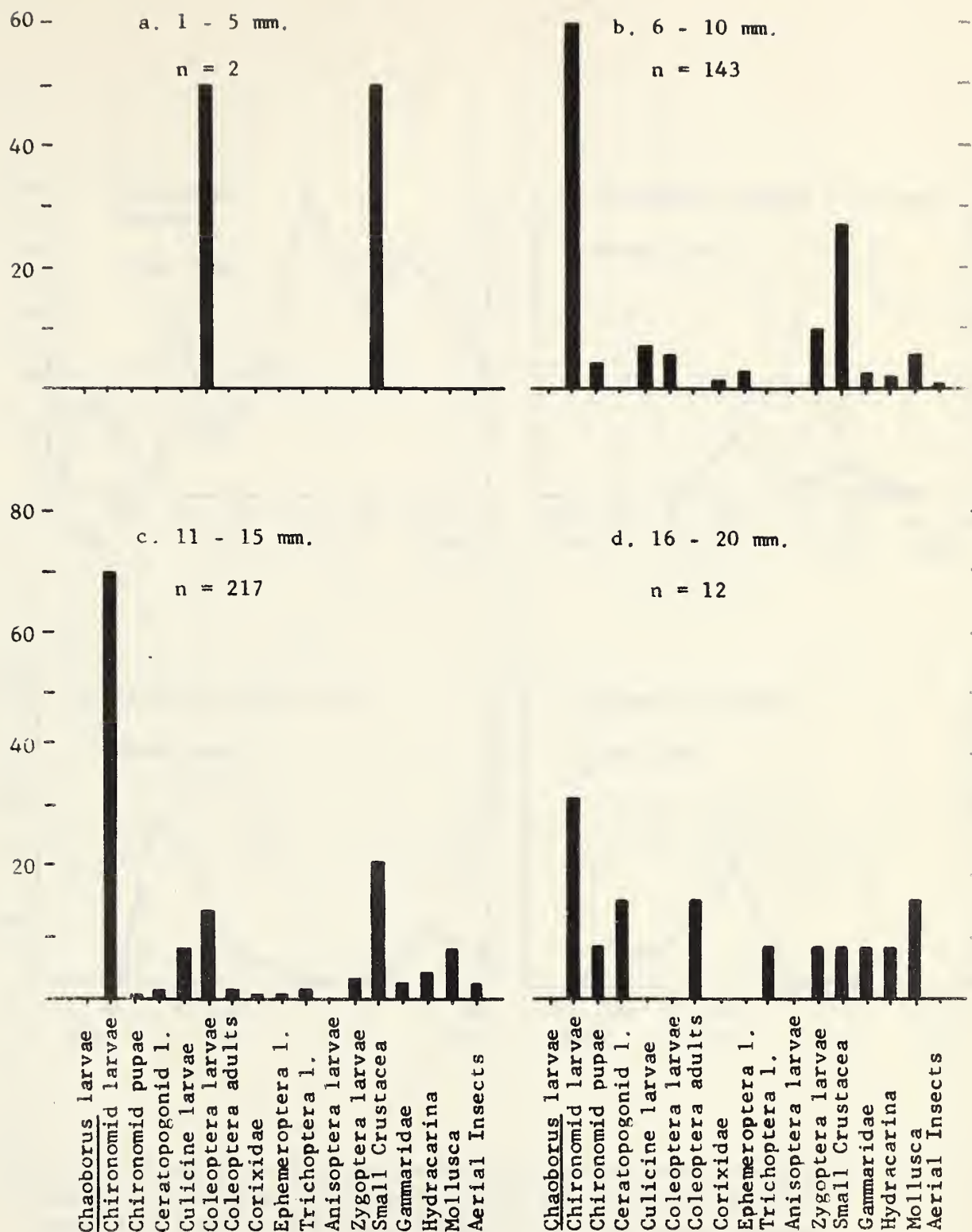


FIG. 33. - The prey of certain size-groups of Leucorrhinia hudsonica.
Units as in FIG. 29.

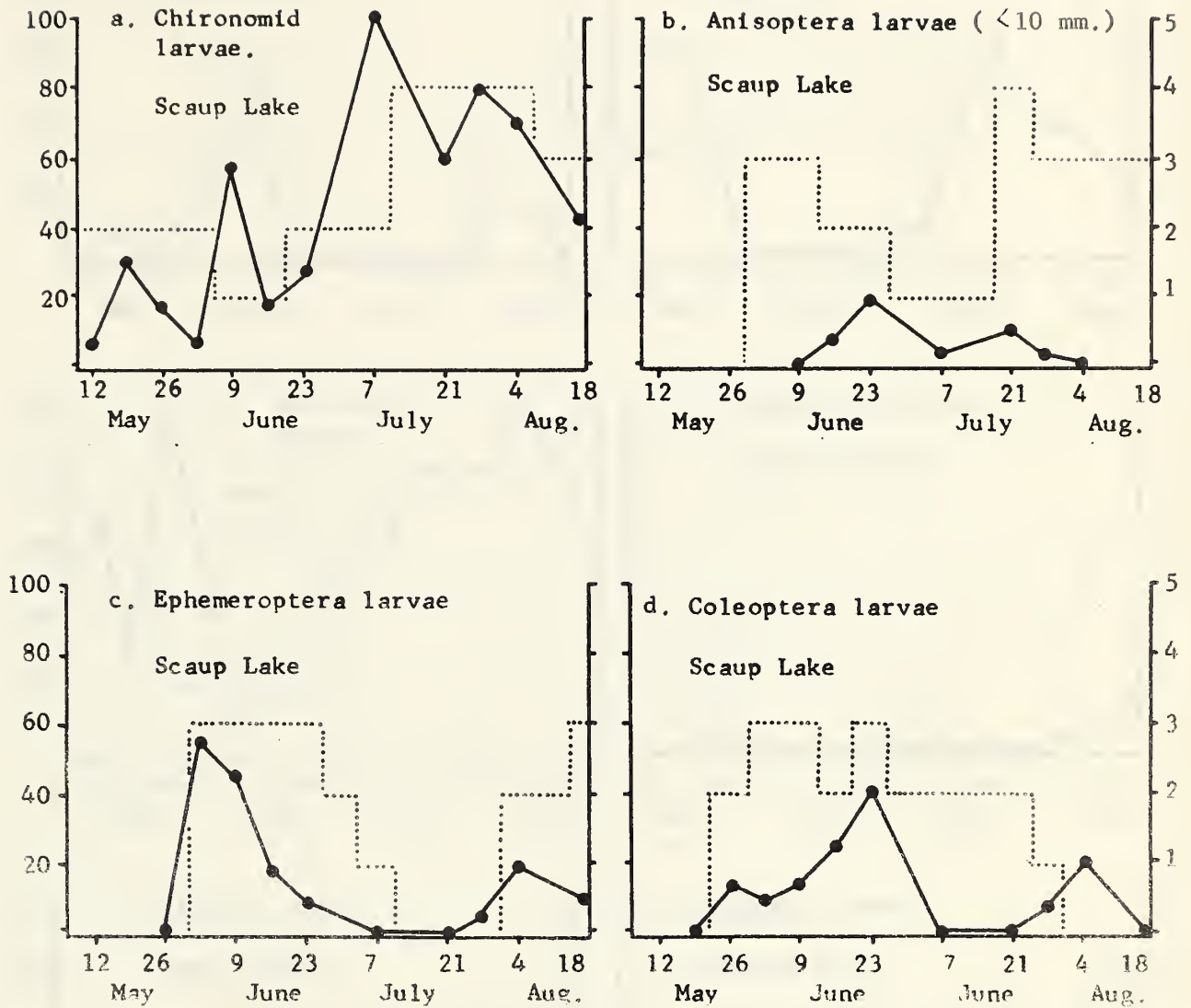


FIG. 34. - Fluctuations in the numbers of certain prey animals in the food of dragonfly larvae from May to August 1962. The solid line represent the occurrence of prey in faecal pellets; units (on left) as in FIG. 29. The dotted line represents the occurrence of prey in the habitat; units (on right) - 1 = rare, 2 = few, 3 = common, 4 = very common, 5 = abundant.

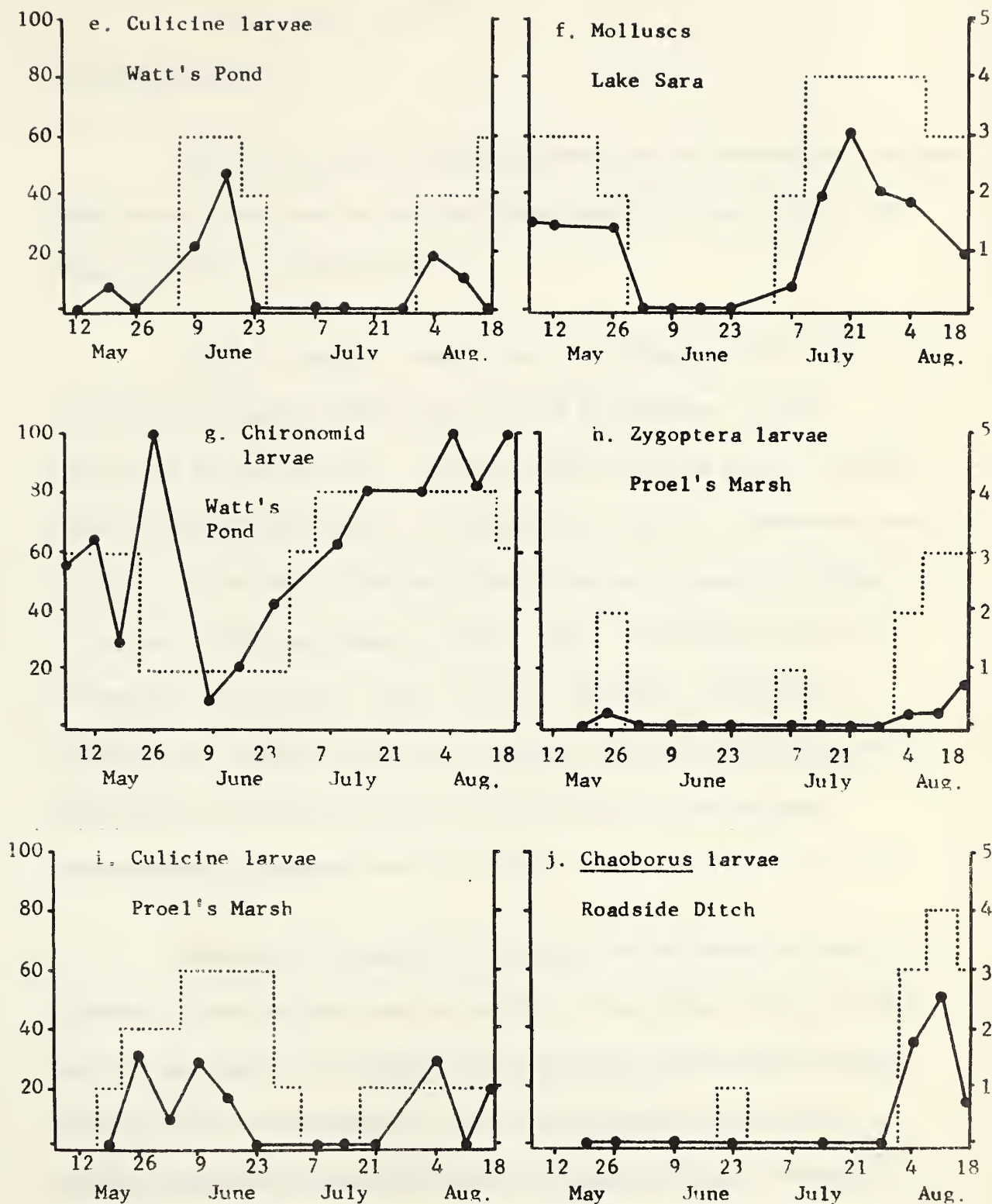


FIG. 34. - cont'd.

6. THE PREY OF DRAGONFLY ADULTS

6.1 Introduction

There are many recorded observations of dragonflies catching large conspicuous prey animals or those which are important to man, either as pests or beneficial forms.

In 1890, Lamborn considered the biological control of Anopheline mosquitoes through the use of dragonflies, though apparently with no success. Poulton (1906) collected several records which included large Diptera, Lepidoptera, Isoptera, Coleoptera, and Odonata, and he drew attention to the inclusion of many forms that are protected through reason of their taste. In the observations of Wesenberg-Lund (1913), moths, Pierids, Syrphids, mosquitoes, Phryganeids, Vespids, and Odonata appear as prey of Aeshnids and Hobby (1933, 1936) has presented lists, drawn up from isolated observations, of dragonflies with prey.

Records of dragonflies feeding on mosquitoes are many, but in most of them the prey was not definitely identified. Tillyard (1917) reports the capture of a Telephlebia godeffroyi Selys with its mouth crammed full with mosquitoes, and Clausen (1940) asserts that smaller Odonates concentrate on these obnoxious flies. Warren (1915) found that definitely identified Culicids formed about 6 per cent

by number of the prey of 24 Anax sp. and less than 2 per cent of the prey of 218 Pantala flavescens. The commonest single component of the prey of Anax in these observations in Hawaii was the honey bee (Apis mellifera L.), followed by Lepidoptera, Coleoptera, and Diptera. Diptera formed half of the food of Pantala and were followed by Lepidoptera (25 per cent) and then Hemiptera, mostly Aphidae.

Apart from the observations made by Warren on gut contents, predation on bees has been noted on several occasions (see e.g. Clausen, 1940; Wright, 1944; Beatty, 1951) often resulting in severe losses to beekeepers (Wright, 1946). Termites, too, fall prey to larger dragonflies such as Coryphaeshna ingens Rambur and Libellula incesta Hagen (Brues, 1947), and the crepuscular Gynacantha nervosa Rambur (Williams, 1937). Bell and Whitcomb (1961) report Erythemis simplicollis Say feeding on the bollworm moth (Heliothis zea (Boddie)) and review previous records of dragonfly predation on Lepidoptera.

In view of the sparse and often spectacular nature of these observations, an attempt has been made to determine the extent to which they reflect the true composition of the diet of adult dragonflies.

6.2 Methods

Dragonflies were collected from various places at different times of day during the summer of 1962. Typical localities collected

from included paths in the bush (Plate 6b), the borders of ponds (Plate 4b), the edges of forests, open fields, and roadsides. The temperature and humidity as recorded by a thermohygrograph in a Stevenson screen, the time of day, and the type of locality, were recorded with each sample. The dragonflies were identified, sexed, and dissected, and the complete guts were removed and their contents examined.

Prey is masticated quickly and thoroughly by the mouthparts and identification of gut contents is very difficult unless a detailed knowledge of the forms that make up the aerial fauna and their salient characters is available. It was considered necessary to take the identification of prey to the ordinal level only, except for special groups such as Culicids which could be identified by their wing scales (Figure 35).

As in the analysis of larval food, the method of frequency of occurrence was used to estimate the relative importance of the different components of the diet.

6.3 The prey of dragonflies in nature; direct observations

Dragonflies can often be seen feeding but their prey is usually so small that it cannot be identified. Observations made in this manner must then be restricted to prey that is large or aggregated. Table 2 is made up of such prey and may be compared with the more

FIG. 35. - Remains of prey found in the guts of adult dragonflies.

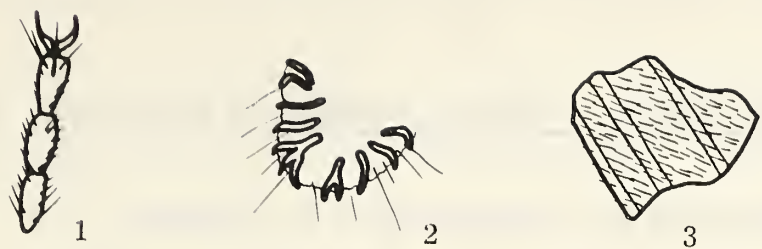
Diptera: 1. Tarsus; 2. Part of labellum; 3. Part of wing; 4. Tarsal claws; 5. Part of leg.

Coleoptera: 6-7. Mandibles; 8. Part of leg.

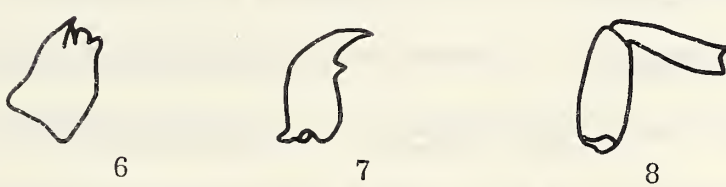
Culicidae: 9. Wing scales.

Simuliidae: 10. Antenna.

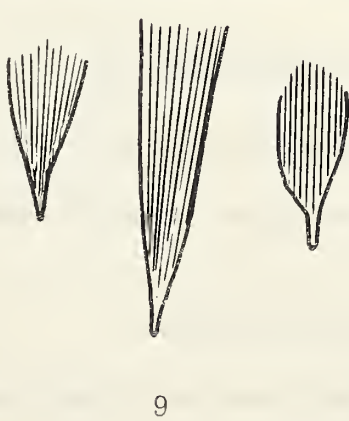
Chironomidae: 11. Part of antenna.



Diptera

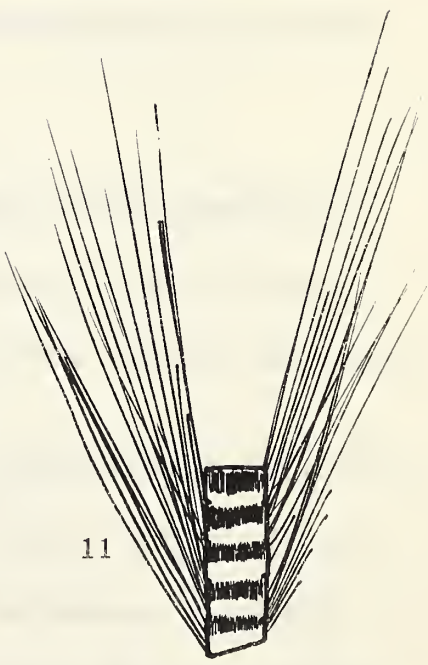


Coleoptera



Culicidae

Simuliidae



Chironomidae

accurate representation obtained from the study of gut contents.

6.4 The prey of dragonflies in nature; analysis of gut contents

It is difficult to go very far with the identification of the finely ground particles that fill a dragonfly's alimentary canal, but the pieces of legs, wings, elytra, etc give an indication of the size of the prey and allow identification at least to the order. A general idea of the food of dragonflies can be formed from this information. The results below were obtained from an examination of 296 guts made up of 54 Cordulia shurtleffi, 16 Leucorrhinia hudsonica, 32 Leucorrhinia proxima, 16 Tetragoneuria spinigera Selys, 1 Libellula quadrimaculata, 127 Sympetrum internum Montgomery, 28 Sympetrum obtrusum Hagen, 3 Aeshna interrupta, 15 Aeshna eremita, and 1 Aeshna umbrosa. Forms which fly at prey from a perch are well represented by the Libellulids, but the Aeshnid sample is rather small.

Small Diptera formed either the whole or the largest part of the food in 94 per cent of the 296 guts. 15 of the 19 Aeshnids had eaten Diptera, whilst 95 per cent of the Libelluloids contained this prey.

Culicids can easily be recognized by their wing scales and 19 per cent of the total sample contained their remains. But this figure depends to a large extent on the time at which the sample was taken, for mosquitoes fly only under certain conditions and their appearance

TABLE 2. - Observations on dragonflies with prey.

Species of dragonfly	Prey	Locality	Date
<u>Aeshna eremita</u>	Zygoptera	Over water	31.vii.62
<u>A. eremita</u>	<u>Sympetrum</u> <u>internum</u>	Roadside	3.viii.62
<u>A. interrupta</u>	Syrphidae	Over water	4.viii.61
<u>A. umbrosa</u>	Ephemeroptera	Over water	ix.61
<u>Cordulia shurtleffi</u>	Chrysopidae	Open field	29.v.62
<u>C. shurtleffi</u>	Teneral Zygoptera	Around lake	31.v-10.vi.62
<u>C. shurtleffi</u>	Trichoptera	Around lake	1.vi.62
<u>C. shurtleffi</u>	Diptera	Sand bank	1.vi.62
<u>C. shurtleffi</u>	Chironomidae	Around lake	4.vi.62
<u>C. shurtleffi</u>	Teneral <u>Leucorrhinia</u> <u>hudsonica</u>	Around lake	4.vi.62
<u>Tetragoneuria</u> <u>spinigera</u>	Simuliidae	Around observer's head	12.vi.62 20.vi.62
<u>Ladona julia</u>	<u>Leucorrhinia</u> <u>proxima</u>	Forest edge	20.vi.62
<u>Sympetrum internum</u>	Simuliidae	Around observer's head	27.viii.62

in the guts of dragonflies can usually be correlated with these conditions. For example, on 7th June 1962 at 1000 hours mosquitoes were common enough along a shaded path in the forest to be a source of annoyance to the collector, and five of seven Cordulia shurtleffi and two of five Leucorrhinia hudsonica collected at this time had eaten them. By 1100 hours the saturation deficiency and the temperature had both risen and Culicids on the wing were then less numerous; only four of ten Cordulia shurtleffi taken in this second sample had eaten them, and in these dragonflies the remains were found in the hind parts of the guts indicating that the mosquitoes had been taken earlier. A large number of the 55 records of predation on mosquitoes were taken early in the day and mostly in sheltered localities.

Other Diptera are more difficult to recognize and definitely identified antennae of Simuliids occurred in only one per cent of the total sample, whilst Chironomid antennae were seen in seven per cent. It is certain, however, that both of these families, especially Chironomids, constitute a much greater part of the diet of dragonflies than these figures suggest.

Next to Diptera, Coleoptera are an important constituent of the food of dragonfly adults, being found in 22 per cent of the guts. Mostly small beetles, many of which are perhaps being carried by wind, are taken. Twenty per cent of the Libelluloids and 58 per cent

of the Aeshnids had eaten them.

Trichoptera occurred only in the guts of large Aeshnids, appearing in 4 of the 19 individuals examined from this family. Other Odonata, too, are probably eaten more by Aeshnids, 2 out of 19 having taken this prey compared with only one of 177 Libelluloids. Lepidoptera do not appear to be an important constituent of the prey of dragonflies in this area.

The wings of small Hymenoptera and Thysanoptera were found in 2 and 2.4 per cent respectively of the total sample, all of the records being from species of Sympetrum. On account of their small size and infrequent occurrence, they contribute little to the food of adult dragonflies in nature.

6.5 Discussion

Dragonfly adults are general insect feeders which take their food from the abundant population of the air. This medium affords them an adequate supply as is shown by the fact that, except for newly emerged individuals, dragonflies collected when weather conditions allow flying usually have their alimentary canals full. They are often attracted to aggregations of their prey but this seems to be merely a spectacular exemplification of the fact that they take whatever prey is most abundant as long as it is of convenient size. As small Diptera

are generally the most abundant, it is not surprising that this order makes up the bulk of the food of dragonflies.

Size is an important consideration and most of the prey is very small, although it does vary with the size of the dragonfly. A greater proportion of large Aeshnids take Coleoptera than do smaller species of dragonflies, and Trichoptera and Odonata occur frequently in the guts of the large forms but rarely, if at all, in those of small- and medium-sized dragonflies. Although few Aeshnids were examined it does appear that, on the whole, they take larger prey than do other species. The large size of these dragonflies makes this possible, and their habit of searching large areas on the wing makes larger prey animals more available to them.

Observations on dragonflies catching prey have been usually directed only to the capture of large insects and most examples in the literature have been made in this manner. This, however, gives a false impression of the importance of large prey animals in the diet. During the first week of June 1962, Cordulia shurtleffi were frequently seen capturing emerging Zygoptera at Lake Sara and they appeared to congregate in the area for this purpose. But all this time they were also feeding on smaller insects, particularly Chironomids, and of 15 C. shurtleffi examined on June 4th, only one had Zygopteran remains in its alimentary canal although all were full of Diptera. The taking

of large prey, although spectacular and apparently frequent, is insignificant compared with the numbers of small Diptera that are eaten.

In the Flatbush area, and undoubtedly elsewhere, it is the belief that dragonflies consume large numbers of mosquitoes, thereby earning the name 'mosquito-hawks'. Dragonflies do indeed catch and eat mosquitoes, often in large numbers (see Wright, 1944), but in the Flatbush area this prey was somewhat protected by the different conditions required for flight by the predators and the prey. Peaks of mosquito flight activity generally occur between 0500 and 0700 hours and between 1800 and 2000 hours (Happold, 1963), light intensity and saturation deficiency being the important factors governing this activity. Mosquitoes fly outside of these times in sheltered places where the saturation deficiency remains low, but they are generally absent from exposed places during the day. Dragonflies, on the other hand, require higher temperatures than exist during the morning period of peak activity of mosquitoes, and they are not normally on the wing until 0800 hours. The overlap in flying times is thus short and although mosquitoes are eaten at this time, this is largely the result of a few dragonflies flying in sheltered places, and relatively little diminution in the numbers of mosquitoes can be expected to occur. In the evening, most dragonflies have gone to rest before the peak of mosquito activity, but species that are capable of crepuscular flight no doubt take mosquitoes at this time.

Mosquitoes may also be taken if they are roused to activity by a drop in the saturation deficiency during the day. Such a situation was noticeable at midday on June 18th 1962 when a sharp drop in saturation deficiency occurred before a short storm. Flying mosquitoes became abundant and five of seven Leucorrhinia proxima and L. hudsonica captured at this time had large numbers of Culicid wing scales in their guts. None were found in dragonflies taken soon after the storm.

7. PREDATORY BEHAVIOUR OF DRAGONFLY LARVAE

7.1 Behaviour patterns

The behaviour patterns shown by dragonfly larvae when catching prey are similar to those of a variety of animals including certain spiders, frogs, mantids, and chameleons, which all use speed to catch prey from ambush. The normal manner in which larvae orientate and catch prey varies between species depending on the stimuli that are important in detecting the prey and the environment in which the larva is living. These normal behaviour patterns are further modified by the physiological state of the larva; the hunger drive, especially, affects the threshold for striking and the speed with which the orientation towards the prey is made, although in nature it is probably only rarely that the hunger drive becomes intense enough to affect the behaviour patterns extensively.

In daylight, all dragonfly larvae usually wait in ambush for prey to come within striking distance. Most Aeshnids live amongst vegetation and during the daytime they are strongly thigmotactic and cling tightly to their supports when disturbed. A number of Aeshna larvae which are kept without supports in the laboratory will hang on to each other in order to satisfy their thigmotactic drives. At night Aeshna larvae leave their supports and walk over the bottom (Paulian

and Serfaty, 1944) and if prey capture takes place at this time the behaviour may be different from that shown in the daytime (see Corbet, 1962). Aeshnids often hang from their supports in an upside-down position (Figure 36), a common feature also of mantid behaviour (Rilling et al., 1959).

Aeshna larvae first detect their prey by means of their well-developed compound eyes, and circular moving objects, 3.5 mm. in diameter (10.0 mm^2 in area), can be sighted at least 15 cm. away. The predator may now stalk its prey, moving very slowly and stealthily and following every move of the prey with its eyes. Continual movement on the part of the prey is not necessary, although larvae may temporarily 'lose' prey when it stops moving (Corbet, 1960). I have, however, had several opportunities to see Aeshna interrupta lineata larvae catching mosquito larvae that were resting at the surface, and have had larvae strike at stationary dummies, although only when the hunger drive was intense.

More normally a larva will not stalk but will remain immobile and wait for the prey to approach closer, following it only with head movements until a short forward move can be made to get the correct range. A starved larva, on the other hand, may rush after the prey or may use jet propulsion to approach it rapidly, although by making these conspicuous movements the chances of

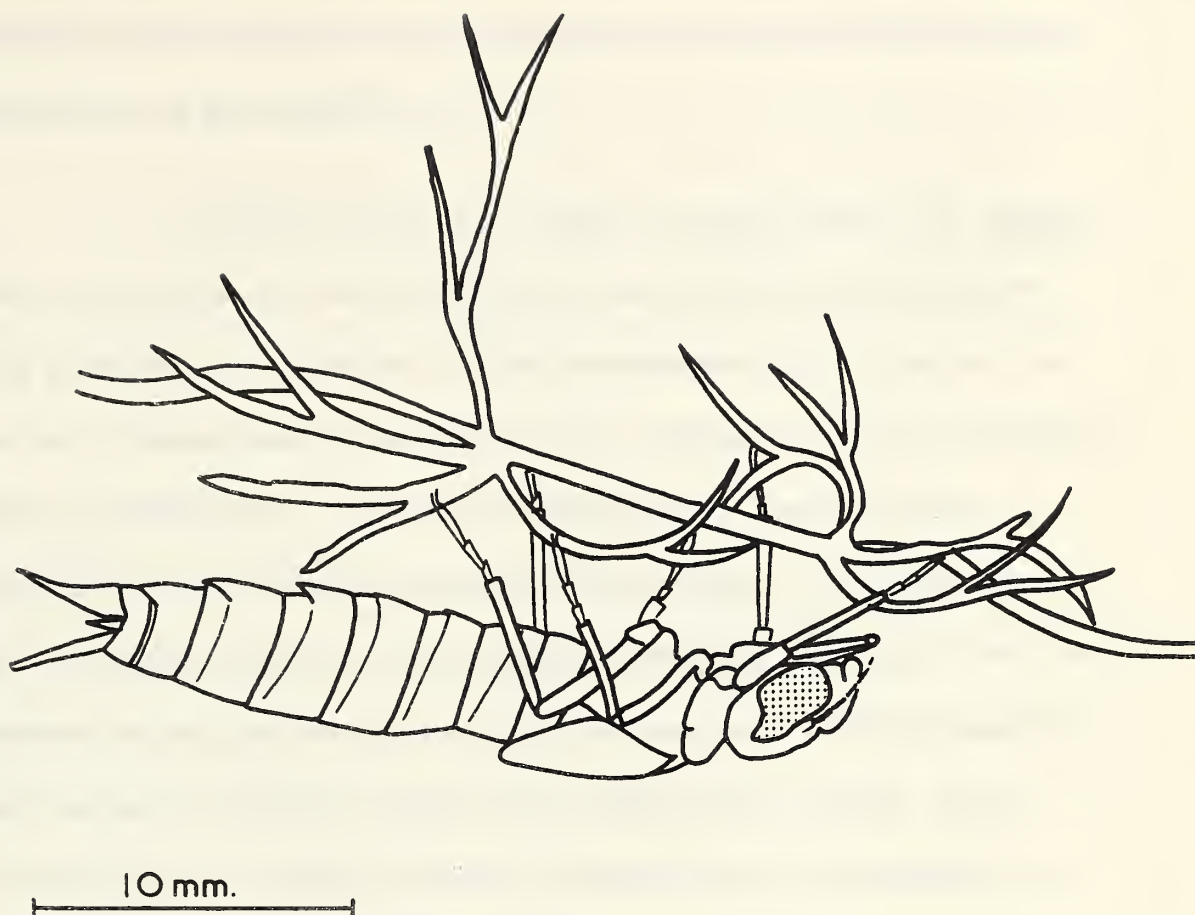


FIG. 36. - Larva of Aeshna interrupta lineata in ambush position.

catching the prey are considerably reduced. Hungry larvae will also climb out of the water to strike at prey. Extremely well fed larvae usually pay no attention to potential prey and may even make escape movements to get away from it.

Provided that the prey does not move quickly, the Aeshna larva, which has cut down the distance between itself and the prey, now prepares for the strike. This demands getting the prey at the correct distance and in the correct line. No control can be exercised over the strike once it has been released as it is so rapid and everything depends on this preliminary alignment. Under normal conditions this localization by Aeshna is probably entirely visual, the distance of the prey being determined by its position on the points of intersection of individual ommatidial axes (Baldus, 1926). This mechanism is most efficient when the prey lies on the median axis of the predator, and an Aeshna larva will usually turn so that it directly faces the prey. Baldus postulated that as the larva of Aeshna cyanea approaches its prey, the ommatidial angle of the part of the eye on which the image falls becomes smaller until it is at its limit of $1^{\circ}12'$ and then the prey is at a distance from the head equal to the length of the extended labium. The last larval instar of Aeshna interrupta lineata has a similar minimum ommatidial angle at the front of the eye (Section 3.2). The strike is not always released when the prey is at a particular distance from the head (Section 7.2), but as

long as the method of distance perception ensures that the strike is not released until the prey is at a distance which is less than the length of the extended labium, then the prey will be caught. This optical fixation on the prey does not apparently take account of small objects between the dragonfly larva and its prey, for larvae will strike at prey which is behind wire gauze, and their attempts to catch prey in more natural habitats are frequently foiled by intervening vegetation.

If prey is moving very fast and appears suddenly in the larva's field of view, there is no time to align properly and the strike may be released at the wrong time or in the wrong direction. It is interesting to note that the sudden appearance of prey from behind and above the head of an Aeshna larva is often a better releaser than prey that appears in front of the head. The large ommatidia on top of the head have a low threshold of response to movement and some of the normal behaviour patterns, during which the larva receives accurate information about the distance and direction of the prey, are bypassed.

When the larva is correctly orientated towards the prey, the labial palps open and the strike usually follows. The palps may, however, open and close again without a strike, or the larva may hesitate for some time with the palps open before striking, showing that even up to this point the behaviour is still plastic. The

success of the strike depends completely on the conduct of the behaviour that has preceded it, for once such actions have been released they are too rapid to be steered (Mittelstaedt, 1957).

The labial palps rapidly close either at the full extension of the labium or, more likely, when the labium is moving forward. The labium is then retracted, bringing the prey to the other mouthparts where it may be rejected or chewed and eaten.

Whilst eating, the threshold for striking is raised and Aeshnid larvae will normally pay no attention to other prey when they are chewing a recent capture. When the hunger drive is strong, however, the threshold for prey capture may not be raised sufficiently and a strike at passing prey may be released even though the labial palps are already holding food. But normally one capture is dealt with at a time and it may be several minutes after completing the consummatory act that the larva will again select an ambush position and become immobile.

Libellulids and Corduliids use tactile as well as visual stimuli to detect their prey (Section 7.43) and the normal behaviour patterns are somewhat different from those of Aeshna. Libellula quadrimaculata and Cordulia shurtleffi live amongst debris on the floor of the pond and, although they can detect prey by visual means alone, they will not leave their well-hidden ambush sites to stalk

prey unless they are very hungry. Normally they remain absolutely motionless until prey comes within striking distance. If prey appears in front of the larva, the head is quickly turned towards the prey animal and the strike follows, and it appears that detection and distance perception are entirely visual.

The ability to respond rapidly and catch prey that stimulates the legs is not shown by the Aeshna larvae that have been studied, but in Libellulids and Corduliids that live amongst debris, this type of behaviour probably leads to the capture of most of their food. The action is so fast that, to the unaided eye, it seems that the labium can be shot out at an angle to the head (see e.g. Gardner, 1956), a phenomenon that would demand great mobility at the labial base. But motion pictures have shown that the head and thorax are turned towards the prey and the labium is extended directly forwards as in Aeshna (Figures 37 and 38).

When strikes are made at prey that is stimulating a hind leg, the fore and middle legs of that side must be moved in order to allow a clear passage for the labium. As the head and thorax bend round, these two legs are raised and folded back along the side of the body and the hind leg may be folded to bring the prey further forward (Figure 39). To allow capture of prey stimulating the middle leg, only the fore leg must be moved and it may either be raised and



FIG. 37. - Larva of *Cordulia shurtleffi* catching a dummy that has stimulated the middle leg. The head and thorax are turned towards the dummy and the fore leg is folded beneath the head. Interval between stages is 15.6 milliseconds. (From 16 mm. motion pictures).

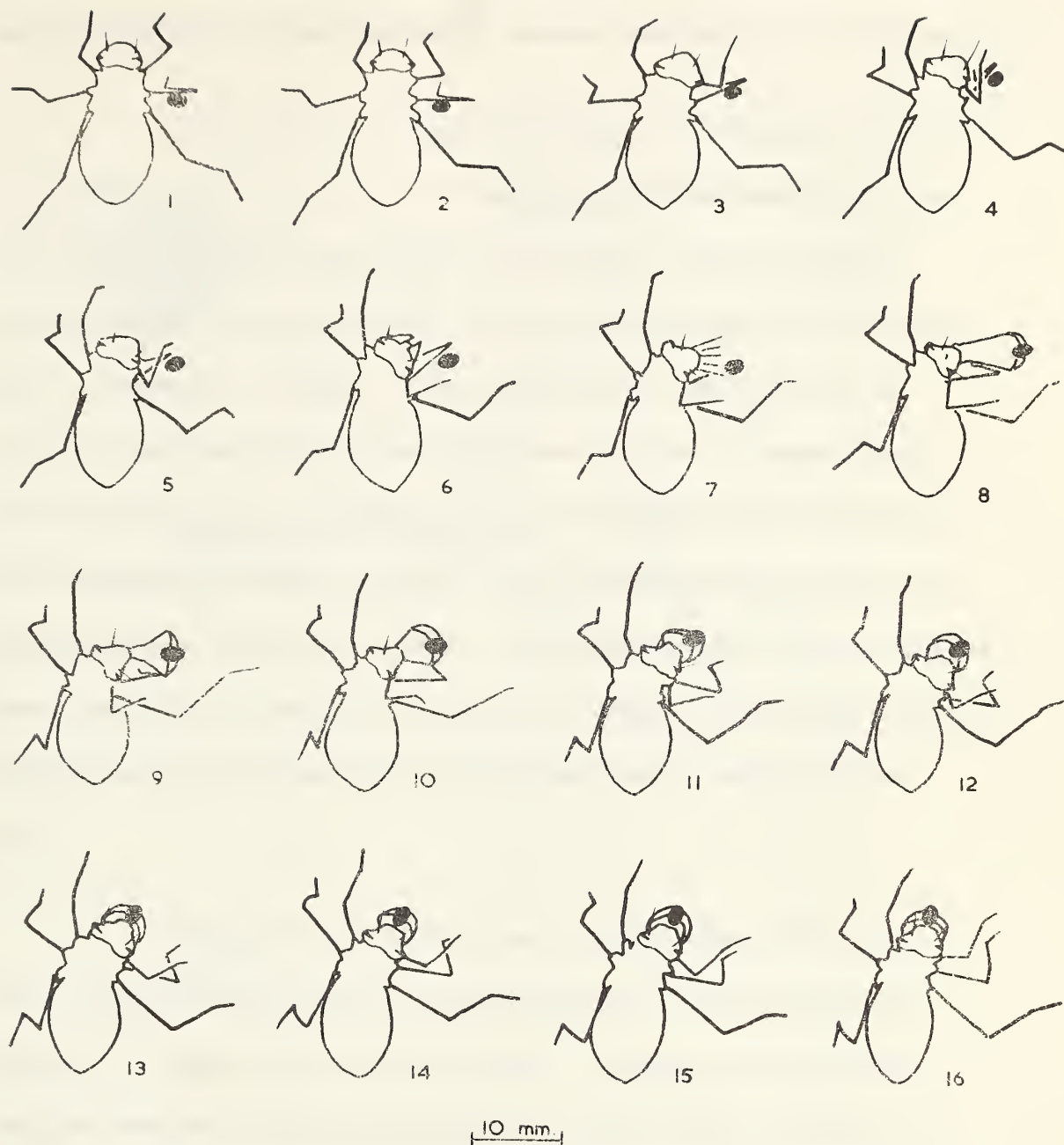


FIG. 38. - As Fig. 37, but the fore leg is folded back along the side of the body.

folded back along the side of the body (Figure 38) or it may be folded beneath the head so that the labium passes over the top of it (Figure 37).

The manner by which the distance and direction of the prey are estimated in these cases is uncertain. Blinded individuals can catch prey accurately from their legs (Section 7.43) and tactile stimuli appear to be all that are required for orientation towards the prey. Normally, however, some information about the prey is probably received by the eyes during the turn, for in experiments with blinded Libellula quadrimaculata, although tactile stimulation alone released accurate strikes, larvae would often rub their eyes with their fore legs after a strike. The performance of such cleaning reactions points to the fact that vision, although not essential, usually plays a part in the behaviour patterns that lead to capture of the prey.

Libelluloid larvae have large labial palps which allow for a certain amount of error in the judgement of the direction of the prey, at least in the vertical plane. In Aeshna, the palps are smaller and the estimation of direction must be more accurate. It is interesting to note that most misses by Aeshna are either above or below the prey. Of 35 photographed strikes by Aeshna eremita only 12 resulted in catches of the dummy, whilst a further 10 resulted in the thread suspending the dummy being caught, and



FIG. 39. - Larva of Cordulia shurtleffi turning to catch a dummy that has stimulated the hind leg. The fore and middle legs are raised and folded back along the body and the hind leg is folded forwards so taking the dummy closer to the head. (From a 35 mm. photograph).

although these may have been aimed at the thread it is also possible that they were directed at the dummy but passed above it; of the clear misses, 10 were below the dummy and 3 were short. The labial palps of Libelluloids perhaps prevent certain errors in this plane, but these tend to be more hurried in their orientation to the prey than Aeshna, and errors of other kinds result in their accuracy being similar to that of the latter genus (Section 7.3).

The estimation of distance is probably less of a problem since prey stimulating the legs is usually within reach of the labium. It would be interesting to see, however, if forms which have very long legs have a correspondingly elongated labium. Fraser (1957) has remarked of Epophthalmia, an oriental genus with legs of great length, that the labium is "the most formidable organ known in the order", with "a very long movable hook and a series of long robust spine-like teeth, which when meshed together remind one of a rat trap".

Climbing forms, such as species of Leucorrhinia and Sympetrum, use their eyes to detect prey and orientate towards it more than do bottom-living species, and their predatory behaviour is often much like that of Aeshna. Last instar Sympetrum danae larvae can detect circular dummies, 3.5 mm. in diameter (10 mm^2), at least 10 cm. away, and if starved they will eject water from the anus to rapidly approach prey and will strike at it several times in quick

succession if it is missed due to careless orientation. In addition, these forms have the ability to respond to tactile stimuli and their predatory behaviour is probably the most versatile and successful in the Order. They can catch prey that is stimulating the bases of the legs in the region of the coxae; this is effected by using the legs to make a jump backwards so that the prey comes to lie in front of the head where it may be caught by the labial palps, either with or without a strike. Prey that is well to the side of the body but touching the hind legs may similarly be captured by means of a jump around so that the larva comes to face the prey. Also these forms may use their legs to spring at prey that is in front of them, in a manner similar to that described by Tillyard (1909) for Diphlebia lestoides (Zygoptera; Amphipterygidae). Attempts to catch objects that are stimulating the dorsal regions of the thorax and abdomen, by throwing back the head and keeping the prementum flexed at 90° to the postmentum, are usually unsuccessful unless the prey is close to the head.

According to Richard (1960b), the young stages of Agrion, Aeshna, and Cordulia all detect prey by mechanical stimuli alone, but as the latter two grow, visual stimuli become important and, in Aeshna, are dominant after the fourth instar. Richard believes that the antennae of Aeshna play a role in the appreciation of the exact distance of labial extension, but in the present study, observations on antennectomized Aeshna interrupta lineata have shown that accuracy is decreased to only

a small extent, an average of 58 per cent success for seven larvae catching mosquito larvae compared with 66 per cent for normal individuals. In Richard's experiments (1960a, 1960b) on Aeshna cyanea, accuracy decreased to 5 per cent for two weeks after antennectomy but then increased to 80 per cent, and it seems probable that the larvae were disturbed by the operation. At any rate, although stimulation of the antennae is a possible aid to the appreciation of distance, Aeshna larvae can catch prey successfully using their eyes alone and a method of distance localization according to the position of the prey on pairs of intersecting ommatidial axes, as proposed by Baldus (1926), is all that is required.

7.2 Details of the strike

The predatory strike of a dragonfly larva is very fast and its details and timing can only be recorded through the use of high-speed motion picture techniques. Attempts to record the strike with a Fastax camera, shooting at speeds between 500 and 1500 frames per second, have not been successful for several reasons. High light intensity is required and this and the heat that usually accompanies it are both unfavourable for normal behaviour by dragonfly larvae. Also, the exact time of the strike is often difficult to predict and shooting at such high speeds involves much wastage of film, a difficulty also experienced by Roeder (1960) whilst photographing

mantids. However, with an appropriate light source such as a 'cold' UV lamp, and a large amount of film it should be possible to obtain ultra-high-speed pictures which would yield much valuable information.

In this study it was possible to obtain pictures suitable for analysis only at 64 frames per second, using conventional Bolex and Bell and Howell 16 mm. cameras. The information obtained from these pictures is somewhat limited, but they have shown a few interesting details of the strike of Anisopteran dragonfly larvae.

When light is available, larvae of the genus Aeshna orientate towards prey only by visual means. These larvae turn until the prey lies more or less in the mid-line, and when close enough to the prey the labium is shot out. The following data are obtained from a study of 34 strikes by eight last instar larvae of Aeshna eremita (Table 3) at circular dummies that were suspended in front of them. Four such strikes, one of which results in a catch, are shown in Plates 7-10.

Prey was struck at when it was from 2.5 to 9 mm. from the front edge of the labrum, the average distance being 4.8 mm. (S.D. = 1.5). The average extension of the labium, measured from the front edge of the labrum to the front edge of the median lobe of the labium, was 6.4 mm. (S.D. = 1.4), with a range of 5 to 9 mm., this latter being the maximum possible extension. Although the labium can be extended to varying distances, this does not seem to be a controlled

TABLE 3. - Details of the strike of Aeshna eremita *

Individual	Catch or Miss	Distance of prey	Time for labial palps to open	Time for forward thrust of labium	Distance of labial extension	Time for retraction of labium	Time for siphon to reopen
1	Mb	4.9	109.2	<31.2	8.8	156.0	202.8
2	Ms	4.2	62.4	15.6	5.3	140.4	171.6
3	C	5.8	78.0	<31.2	4.9	187.2	156.0
4	Ct	2.6	46.8	<31.2	7.5	124.8	?
5	Mb	6.6	?	15.6	6.6	109.2	-
6	C	5.8	124.8	<31.2	5.8	218.4	62.4
7	Mb	4.9	46.8	15.6	5.8	124.8	202.8
8	C	4.9	124.8	<31.2	7.5	218.4	?
9	C	4.9	62.4	15.6	4.9	140.4	270.8
10	C	3.5	46.8	<31.2	3.5	140.4	270.8
11	Mb	2.5	62.4	15.6	3.6	78.0	171.6
12	C	2.0	109.2	<31.2	2.5	156.0	234.0
13	Ct	2.9	78.0	15.6	5.9	156.0	?
14	C	5.1	78.0	<31.2	6.3	140.4	?
15	Mb	4.2	62.4	15.6	5.6	124.8	156.0
16	C	4.7	46.8	<31.2	5.4	109.2	109.2
17	Mb	5.9	109.2	<31.2	6.4	156.0	109.2
18	Mb	2.5	93.6	<31.2	5.6	140.4	124.8

* From 16 mm. motion pictures; times based on 1 frame = 15.6 milliseconds.
 C = catch of dummy; Ct = catch of thread; Mb = miss below; Ms = miss short.
 Distances are measured in millimetres.

TABLE 3. - cont'd. *

Individual	Catch or Miss	Distance of prey	Time for labial palps to open	Time for forward thrust of labium	Distance of labial extension	Time for retraction of labium	Time for siphon to reopen
19	Mb	3.2	109.2	<31.2	5.1	156.0	78.0
20	C	4.9	93.6	<31.2	6.1	171.6	124.8
21	Mb	2.9	109.2	<31.2	6.8	140.4	?
22	Ms	5.4	78.0	15.6	6.9	156.0	62.4
23	Ct	5.1	109.2	<31.2	7.3	218.4	15.6
24	Ct	?	?	?	7.6	31.2	31.2
25	Ct	5.4	62.4	<31.2	6.8	124.8	15.6
26	Ct	?	?	15.6	?	62.4	62.4
27	C	4.4	46.8	<31.2	6.3	78.0	62.4
28	Ct	5.7	?	15.6	6.3	62.4	31.2
29	M	7.9	124.8	<31.2	7.9	218.4	156.0
30	Ct	5.2	156.0	15.6	5.5	218.4	46.8
31	Mb	4.8	93.6	<31.2	7.2	218.4	-
32	C	5.1	31.2	<31.2	5.1	218.4	-
33	Ct	3.5	31.2	15.6	6.4	109.2	31.2
34	C	8.9	15.6	15.6	8.9	78.0	-

* From 16 mm. motion pictures; times based on 1 frame = 15.6 milliseconds.

C = catch of dummy; Ct = catch of thread; Mb = miss below; Ms = miss short.

Distances are measured in millimetres.

action since it is not correlated with the distance of the prey. The labium was usually extended further than the distance of the prey, ensuring that the prementum would hit the prey and the open palps could close on it, assuming that the judgement of direction had been correct.

The strike may be divided into four stages: the opening of the palps, the forward thrust of the labium, the closing of the palps, and the retraction of the labium. The labial palps open before the labium swings forward, and this first action takes from 15 to 150 milliseconds with an average of 80 milliseconds. When the palps are fully open, the postmentum swings forward and the prementum unfolds. Because of the slow speed at which these pictures were taken it is difficult to get an accurate timing on this action, but it seems certain that the labium reaches its full extent in less than 30 milliseconds, probably between 15 and 20 milliseconds. This time also includes the closing of the labial palps which has not been observed in these pictures. The labium is retracted in 60 to 220 milliseconds, the average time for this stage being 142 milliseconds (S.D. = 48). There is no significant difference between the time for retraction after a catch and that after a miss. The complete operation from the start of abduction of the palps to the complete retraction of the labium will thus take, on the average, about one quarter of a second.

One interesting phenomenon which this film has shown is the closing of the anal siphon. Generally the anus closes as the

labial palps open and complete apposition of the epiproct and paraprocts occurs either exactly at the time of the strike or 15 to 20 milliseconds thereafter. The siphon then reopens in 15 to 270 milliseconds, the average being 118 milliseconds (S.D. = 78). As mentioned in Section 2.2 this would seem to be an aid to the hydraulic mechanism of labial extension.

The above details are generalized but, as always when dealing with animals, one comes across examples which still do not conform in spite of the broad generality already allowed. There are times when the palps open in readiness for a strike, but then close without the strike being released. The postmentum may even fold forward somewhat but the prementum does not unfold and the forward thrust does not follow. Then I have one record of the labium being retracted in about 30 milliseconds, almost as fast as it is extended. Then again, the siphon does not always close completely, especially when the larva swims towards the prey by jet propulsion and strikes from a swimming position. But these are abnormal and the behaviour patterns associated with the strike are quite stable even if the timing of the various stages is very variable.

It is interesting to compare the times for Aeshna with those obtained by Roeder (1960) for the praying mantis Hierodula. In the mantis, the prey is hit about 60 milliseconds after the strike

commences, somewhat faster than the time taken to hit prey from the start of palp extension in Aeshna. However, all of this time in mantids is occupied by the strike, whereas in Aeshna the actual forward movement of the labium takes only about 20 milliseconds, even though it is operating in a more viscous medium. This difference may be correlated with the respective mechanisms, for the mantis legs are large and are operated by muscles, whilst the dragonfly labium is small and is hydraulically operated.

In Cordulia shurtleffi and Leucorrhinia hudsonica (Tables 4 & 5) all stages of the strike are more rapid than the corresponding stages in Aeshna eremita. The palps of Cordulia shurtleffi open in about 15 milliseconds and the strike is complete within a further 15 milliseconds. Retraction of the labium then takes from 46 to 156 milliseconds with an average of 114 milliseconds. Leucorrhinia hudsonica strikes even faster and the opening of the palps and the forward thrust of the labium could not be separated at the speed at which the pictures were taken, and it appears that both actions combined take less than 15 milliseconds. The faster strike of Leucorrhinia hudsonica may be correlated with the smaller size of the labium.

When Cordulia shurtleffi strikes at prey that is in front of the head, the strike either being released visually or by stimulation

TABLE 4. - Details of the strike of Cordulia shurtleffi *

Individual	Position of prey	Catch or Miss	Time for turn	Distance of prey	Time for labial palps to open	Time for strike	Distance of labial extension	Time for retraction of labium
1	R. meso-tibia	C	78.0	1.9	31.2	15.6	5.7	156.0
2	In front	C	-	2.8	15.6	15.6	4.8	124.8
3	In front	C	-	2.3	15.6	15.6	5.7	109.2
4	R. meso-tibia	C	62.4	2.3	15.6	15.6	6.6	140.4
5	R. meso-tarsus	C	31.2	6.6	15.6	15.6	6.6	46.8
6	L. meso-tibia	C	78.0	2.8	15.6	15.6	5.1	109.2

* From 16 mm. motion pictures; times based on 1 frame = 15.6 milliseconds.
Distances are measured in millimetres. C = catch of dummy prey.

TABLE 5. - Details of the strike of Leucorrhinia hudsonica *

Individual	Position of prey	Catch or Miss	Time for turn	Distance of prey	Time for opening of labial palps and strike	Distance of labial extension	Time for retraction of labium
1	L. pro-tarsus	C	31.2	2.6	15.6	3.0	46.8
2	R. meso-tibia	M	31.2	2.0	15.6	4.4	46.8
3	L. pro-tibia	M	31.2	0.6	15.6	2.0	31.2
4	L. meso-femur	M	15.6	?	15.6	1.0	78.0
5	R. pro-femur	M	15.6	1.0	15.6	2.0	102.4
6	L. pro-tibia	C	15.6	2.0	15.6	3.0	46.8
7	L. meso-	C	31.2	?	15.6	?	156.0

* From 16 mm. motion pictures; times based on 1 frame = 15.6 milliseconds.
Distances are measured in millimetres. C = catch; M = miss.

of the antennae, this prey will be in a position to be chewed in about 150 milliseconds. When prey is caught from the legs, however, the head has to be turned so that the labium can be shot directly out at the prey and this turning action takes a further 30 to 80 milliseconds.

Similarly Leucorrhinia hudsonica must turn the head and thorax before prey, which has stimulated the legs, can be caught. In this species, the action is quicker than in C. shurtleffi and takes only 15 to 30 milliseconds.

The labial palps of Libelluloid dragonfly larvae are large and prey animals would receive warning of the strike if the palps were to open slowly. The evolution of a faster action would thus be a greater advantage to these larvae than to Aeshnids whose palps are smaller. It seems likely that Libelluloids at first caught prey only in front of the head, either after detecting the prey visually or after antennal stimulation, and that the opening of the palps was already rapid before the capacity to turn the head and catch prey from the legs was evolved. The extra time needed to turn could then be safely taken due to the already very rapid nature of the strike. The evolution of a rapid opening of the palps whilst prey was already being caught from the legs seems less likely, as the opening of the palps could be accomplished during the turn, unless, perhaps, orientation towards the prey must be complete before the next action in the behaviour chain can commence.



Plate 7. - The strike of the larva of *Aeshna eremita* seen from above. The labium is extended in frame 10 and it passes below the dummy. Interval between frames, 15.6 milliseconds.

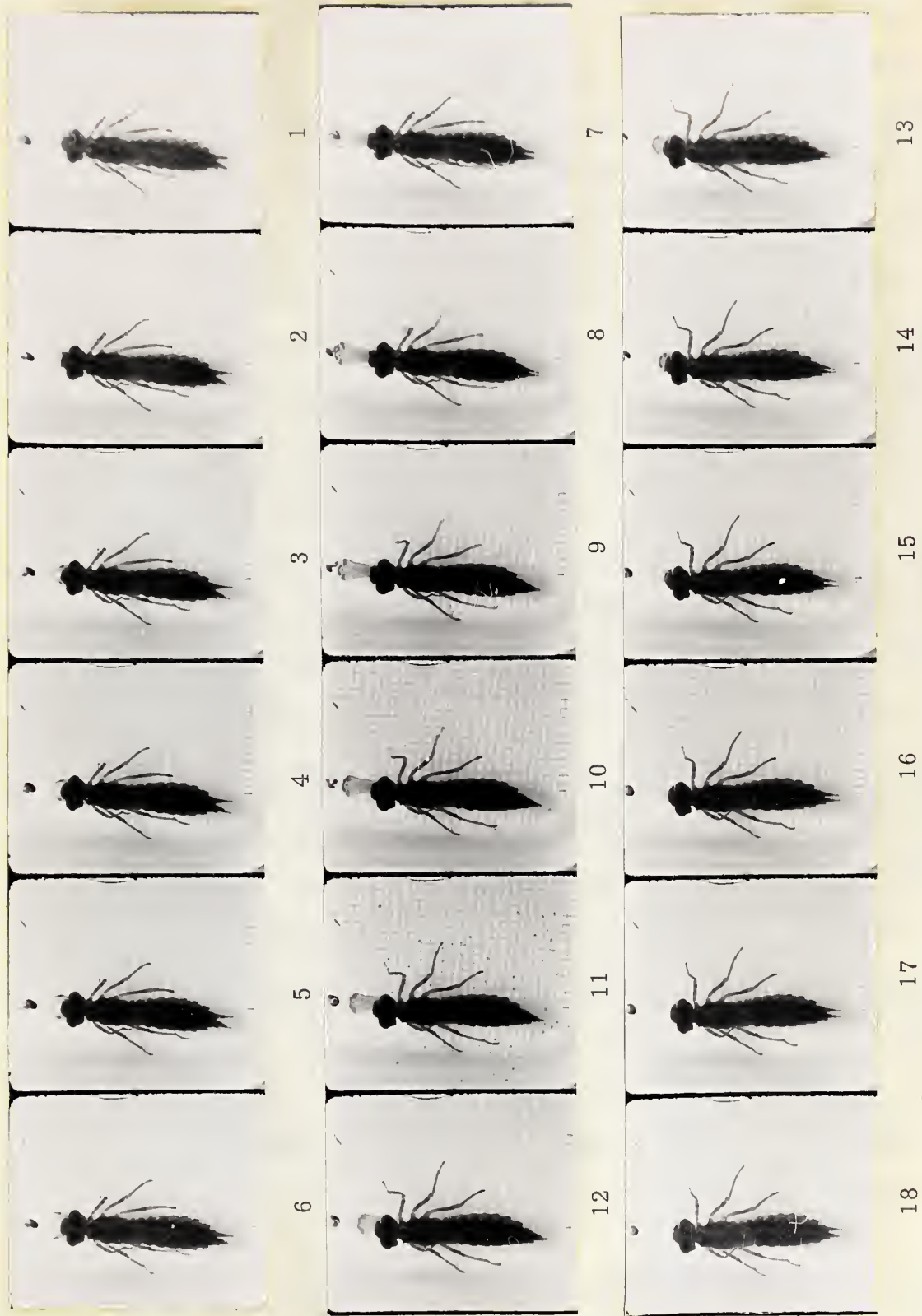


Plate 8. - The strike of the larva of Aeshna eremita seen from above. The labium is extended between frames 6 and 7 and it passes below the dummy. Interval between frames, 15.6 milliseconds.

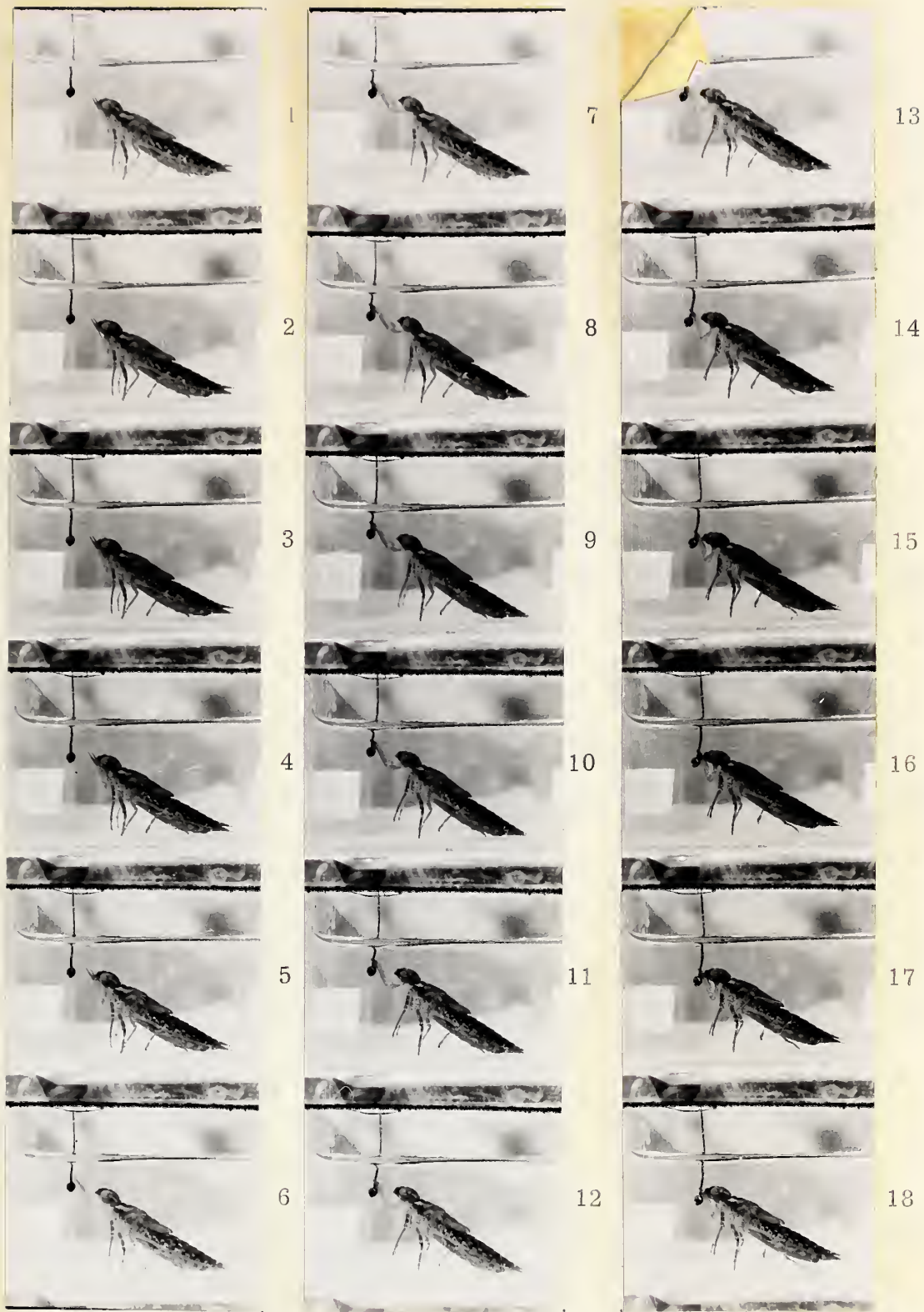


Plate 9. - The strike of the larva of *Aeshna eremita* seen from the side. The labium is extended in frame 6 and the thread suspending the dummy is caught. Interval between frames, 15.6 milliseconds.

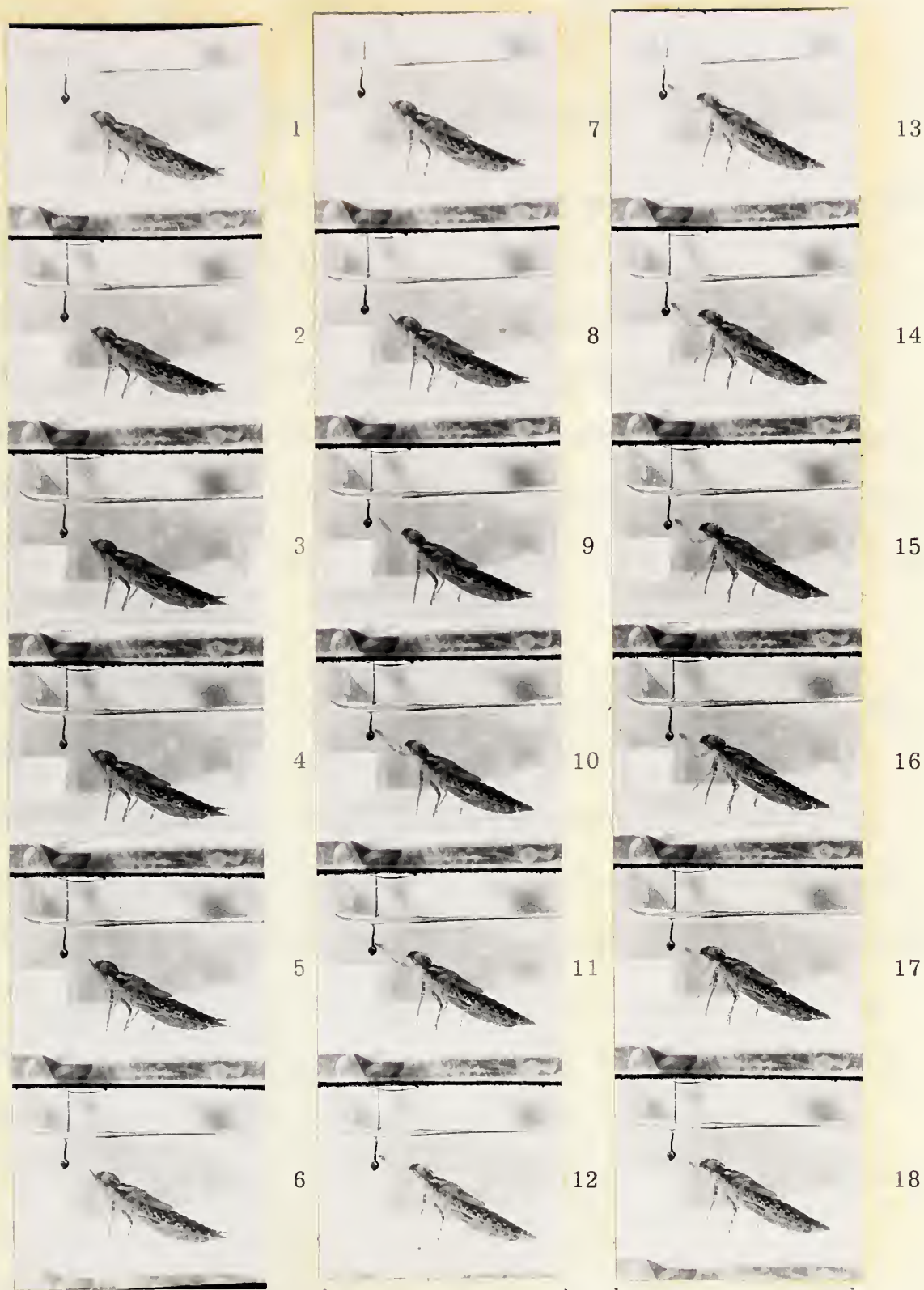


Plate 10. - The strike of the larva of *Aeshna eremita* seen from the side. The labium is extended in frame 9 and it falls short and slightly above the dummy. Interval between frames, 15.6 milliseconds.

7.3 The accuracy shown by dragonfly larvae in catching prey

The proportion of strikes that result in a catch is affected by the size and the activity of the prey. Experiments were carried out using fairly small, slow-moving prey (mosquito larvae) and larger, fast-moving prey (Gammarids). Each dragonfly larva was allowed twenty strikes in order to assess its performance and only prey that was caught and held by the labium was recorded as a catch; prey that was hit by the labium but was not held, and thus escaped, was recorded as a miss.

Systematic observations have not been made on very slow-moving prey such as Trichoptera larvae, but I have never seen a dragonfly larva err in its attack on one of these creatures; there is no reason why attacks on such slow-moving prey, assuming that it is within favourable size limits, should not result in 100 per cent success. When prey is moving, however, errors in the judgement of both the distance and the direction of the prey occur, due in part to the often hurried nature of the attack and in part to the movement of the prey itself. Observations on the capture of mosquito larvae by five species of dragonfly larvae, ranging in average size from 15 to 30.5 mm., showed them to be successful in 60 to 75 per cent of their attacks (Table 6).

Gammarids are more difficult to catch than mosquito larvae because they are larger and faster, and their hard, smooth

TABLE 6 . - The accuracy shown by dragonfly larvae in catching prey

Species of dragonfly larva	Number of larvae	Average size, mm.	Average percentage catch
a) Mosquito larvae as prey			
<u>Aeshna interrupta lineata</u>	7	15.5	66
<u>Aeshna interrupta lineata</u>	10	30.5	66
<u>Leucorrhinia hudsonica</u>	5	15.0	63
<u>Leucorrhinia proxima</u>	10	18.5	74
<u>Libellula quadrimaculata</u>	5	21.5	69
<u>Sympetrum danae</u>	14	15.0	60
b) Gammarids as prey			
<u>Leucorrhinia hudsonica</u>	5	15.0	25
<u>Leucorrhinia proxima</u>	10	19.0	26
<u>Libellula quadrimaculata</u>	8	22.5	28

cuticle makes it difficult for the labial palps of the predator to maintain a firm hold. Thus, three species of Libellulid larvae were successful in only 25 to 28 per cent of their attacks on Gammarids (Table 6).

As the reaction times of both predator and prey are likely to be of the same order of magnitude (Roeder, 1959), a miss by a larva striking from ambush is likely to be due to a misjudgement on the part of the predator rather than a true escape movement on the part of the prey.

7.4 The stimuli that affect the release of the strike

7.41 Introduction

The predatory behaviour of dragonfly larvae is largely governed by characters of the prey. Baldus (1926) has investigated certain aspects of prey recognition by dragonfly larvae, Koehler (1924) has examined colour vision in Aeshna cyanea, and Alverdes (1924) has studied sensory perception in the Zygoptera, whilst Sälzle (1932), Gaffron (1934), and Tonner (1938) worked on the perception of movement by dragonfly larvae. More recently, Richard (1960a, 1960b) has investigated the relative importance of visual and mechanical stimuli to Odonate larvae.

In this section, experiments designed to test the relative

strike-releasing values of various external factors are described.

7.42 Visual stimuli

Paper dummies were used to estimate the importance of various characters of the prey, the methods being similar to those used by Rilling, Mittelstaedt and Roeder (1959) on mantids.

Some difficulty is experienced in standardizing experiments of this sort. The method of introducing the dummy can be standardized by careful control of one's technique, but variations introduced by the animals themselves are more difficult to control. The manner in which the physiological state of an animal affects its predatory behaviour has been observed by Kramer (1960) in mantids and his remarks apply equally well to dragonfly larvae. Larvae will not feed when they are interfered with by the experimenter or by other animals, when they are about to moult, or during metamorphosis to the adult. If they are greatly disturbed or if they are not hungry they react to even small prey with rapid escape movements. Hunger greatly affects behaviour, for a very hungry larva will strike at floating pieces of debris, whilst a satiated larva will ignore potential prey. Added to this is the variation between individuals which must be controlled as effectively as possible by performing several experiments on several larvae.

Larvae were kept in enamel photographic trays for the experiments. A piece of nylon gauze provided a foothold and each larva was allowed the freedom of the dish. The experimenter was hidden from the larva by a cardboard shield around the dish and the dummies were suspended by cotton threads and introduced from above. The dummies were moved in front of the dragonfly larva in a manner which attempted to simulate, as far as possible, the movements of a real prey animal.

Experimental animals were kept in approximately the same states of hunger during experiments. They were isolated three days before the experiment and were not fed from this time on. When a dummy was introduced a larva would usually strike readily at first, but the frequency rapidly decreased until stimulus satiation. When an animal would no longer strike at a dummy that trial was concluded and the number of strikes before satiation was taken as an expression of the strike-releasing value of the dummy.

Consecutive trials were separated by periods of sixty minutes, as it appeared that recovery from the previous dummy was complete by this time. This was considered preferable to conducting trials at longer intervals when changes in other facets of the physiological state of the larvae would have introduced other errors. As an added precaution, the possibility that recovery is not complete

by this time was compensated by randomization of the order in which the dummies were presented to each larva.

In order that the effects of very active larvae should not over-shadow those of relatively inactive larvae and thus make the randomization ineffective, the results were adjusted by assigning the value of 100 to the highest result in each experiment and grading the others accordingly. For statistical analysis the percentages were converted to angles before applying the appropriate statistical test. Duncan's multiple range test (Duncan 1955) was used to determine where significant differences lay.

a. Movement

Movement of prey has been considered to be of importance to several predatory animals in the identification of potential food; Blunck (1924) showed that larvae of Dysticus react to this stimulus, Rilling et al. (1959) found it to be important to mantids, and Drees (1952) refers to its importance to salticid spiders. The value of this stimulus to dragonfly larvae has been observed by Baldus (1926), Gaffron (1934), and Tonner (1938).

The statement that dragonfly larvae will only strike at moving prey is not strictly correct as they will strike at stationary objects that have recently been moving. However, movement of the prey at some time during preparation for the strike does seem to

be essential.

In order to obtain a definite indication of the value of different kinds of movement in eliciting striking, a circular black dummy, 2 mm. in diameter (3 mm.^2), was presented against a white background to Aeshna eremita and Leucorrhinia hudsonica larvae in three ways: a) the dummy was smoothly swung in front of the larva; b) the dummy was swung in front of the larva as in a) but with a regular vertical oscillation of about 4 mm. and a frequency of about 3 cycles per second; and c) the dummy was moved with a faster, jerky, non-regular rhythm. The results are shown in Tables 7 and 8.

The smoothly swinging dummies were struck at on a few occasions but were usually ignored. These zero values were, however, real and not an effect of the physiological state of the larva blocking all reactions, since change from this smooth rhythm to a jerky rhythm always provoked the strike immediately.

Twelve experiments were carried out on Aeshna eremita larvae, which struck at the smoothly swinging dummy on one occasion only. Student's t-test showed the difference between the number of strikes made at the regularly oscillating dummy and those made at the jerky dummy to be significant at $P < 0.001$. In twelve experiments on six Leucorrhinia hudsonica larvae the smoothly swinging dummies were attacked on six occasions although all were low strike rates.

TABLE 7. - The effect of movement of dummy prey on the number of strikes made by larvae of Aeshna eremita.

Individual	Strike-releasing values of various kinds of movement *		
	smooth movement	regularly oscillating movement	jerky movement
1	0	80	100(20)
2	0	31	100(26)
3	0	64	100(14)
4	0	39	100(28)
5	0	18	100(17)
6	0	65	100(26)
7	0	42	100(19)
8	0	32	100(25)
9	0	18	100(40)
10	0	23	100(13)
11	4	18	100(51)
12	0	48	100(27)

* The strike-releasing values for each stimulus are obtained from the number of strikes to stimulus satiation by awarding the value of 100 to the highest number with each individual and grading the others accordingly. The numbers in parentheses are the actual numbers of strikes to stimulus satiation.

TABLE 8. - The effect of movement of dummy prey on the number of strikes made by larvae of Leucorrhinia hudsonica.

Individual	Strike-releasing values of various kinds of movement *		
	smooth movement	regularly oscillating movement	jerky movement
1	7	43	100(28)
2	0	44	100(9)
3	8	36	100(39)
4	4	27	100(70)
5	0	86	100(7)
6	0	26	100(34)
7	0	47	100(19)
8	0	100(6)	67
9	0	17	100(24)
10	8	21	100(450)
11	1	13	100(149)
12	3	2	100(276)

* See footnote TABLE 7, p. 203.

Again the difference between the number of strikes made at the smoothly swinging dummy and those made at the jerky dummy was significant at $P < 0.001$.

Clearly the strike is released more readily at a moving object than at a stationary object. But these experiments show that the type of movement also affects the behaviour. The response to 'smooth movement' is little more than that to 'no movement', but a regularly oscillating movement will always release the attack unless the larva is completely satiated, whilst a rapid jerky movement is most effective in releasing the strike. In nature, however, the physiological state of the larva appears to be such that slow moving objects will usually release the strike, for snails frequently appear in the food (Section 5). Gastropods do, however, move somewhat jerkily at times when they are creeping over vegetation, the shell often being pulled over quite rapidly, and once a larva has detected and fixed on an object it often takes very little, if any, extra movement on the part of that object to bring about the release of the strike.

Assuming that the moving object is within favourable limits of size, presumably it is the speed with which different ommatidia are stimulated that is the important underlying phenomenon governing strike behaviour. The importance of this response to movement in nature is plain. Dragonfly larvae are purely carnivorous animals and the prime observable factor distinguishing animal life being movement

it is a logical advantage for any predacious animal to react strongly and positively towards this stimulus.

b. Size

White circular dummies of diameters from 0.5 mm.

upwards were presented against a black background to larvae of Aeshna interrupta lineata and Libellula quadrimaculata. For a particular larva of a certain size under a given set of conditions, there are both upper and lower limits to the size of the prey that it will attack. The smallest dummy used in these experiments was 0.2 mm^2 . ($d = 0.5 \text{ mm.}$) and, under the conditions of the experiments, was apparently not at the lower limit for either A. interrupta lineata (13-15 mm. in length) or L. quadrimaculata (18 mm. in length).

An upper limit could, however, be obtained. For ten of twelve A. interrupta lineata the upper limit was 20 mm^2 . ($d = 5 \text{ mm.}$) and these larvae would not strike at dummies 28 mm^2 . in area ($d = 6 \text{ mm.}$); for the other two individuals the limit was 28 mm^2 . and dummies of 38 mm^2 . ($d = 7 \text{ mm.}$) were not struck at. The upper limit for L. quadrimaculata under the same experimental conditions was more variable. Four individuals struck at dummies of 38 mm^2 . but not at those of 50 mm^2 . ($d = 8 \text{ mm.}$); one individual struck at dummies of 50 mm^2 . but not at those 64 mm^2 . in area ($d = 9 \text{ mm.}$); four individuals struck at dummies of 64 mm^2 . but not at those of 78 mm^2 . ($d = 10 \text{ mm.}$); and one individual struck at dummies of 78 mm^2 . but

not at those 95 mm². in area (d = 11 mm.). In review, the overall range for ten A. interrupta lineata was 0.2-28 mm². and that for ten L. quadrimaculata was 0.2-78 mm².

Application of the Analysis of Variance and Duncan's test showed that A. interrupta lineata preferred dummies 3 mm². in area (d = 2 mm.) to those of 0.8 mm². (d = 1 mm.) and 7 mm². (d = 3 mm.), which were in turn preferred to those of 10 mm². (d = 3.5 mm.) and 12 mm². (d = 4 mm.), and dummies 0.2 and 20 mm². in area were least preferred (Table 9, Figure 40). The order of preference in L. quadrimaculata was not as distinct but dummies between 0.2 mm². and 12 mm². in area were preferred to those between 20 and 38 mm². (Table 10; Figure 40).

In nature, dragonfly larvae will only attack prey which falls between certain size limits. The lower limit ensures that energy is not wasted on prey that would yield little food value, and the upper limit ensures that an attack is not released against an animal that is too large to be handled conveniently, including those which could in turn attack the dragonfly larva should its presence be revealed. These limits vary according to the size of the larva and are also affected by its inner state, especially the hunger drive. One Aeshna interrupta lineata larva, which was observed in the laboratory, lived for 59 days without food and although there was much variation in the size of the largest dummy that would be struck at, there was a general trend to striking at

TABLE 9. - The effect of size of prey on the number of strikes made
by larvae of Aeshna interrupta lineata.

Individual	Strike-releasing values of various sizes (mm ² .) of circular dummies *						
	0.2	0.8	3	7	10	12	20
1	5	100 (130)	86	31	36	10	2
2	2	100 (128)	96	66	46	28	2
3	6	100 (84)	98	25	10	6	4
4	23	100 (61)	70	28	16	21	2
5	8	12	100 (26)	73	35	58	12
6	12	88	100 (16)	62	56	19	6
7	7	85	100 (61)	56	16	3	3
8	2	100 (106)	78	71	67	65	9
9	3	36	100 (39)	100 (39)	10	41	5
10	2	5	100 (40)	62	12	52	5

* See footnote TABLE 7, p. 203.

TABLE 10. - The effect of size of dummy prey on the number of strikes made by larvae of Libellula quadrimaculata.

Individual	Strike-releasing values of various sizes (mm ² .) of circular dummies *							
	0.2	0.8	3	7	12	20	28	38
1	100 (48)	94	100 (48)	77	60	79	38	6
2	62	67	29	100 (21)	29	67	5	5
3	58	59	47	38	100 (64)	3	16	5
4	66	55	74	100 (235)	69	24	16	12
5	49	100 (57)	68	28	21	26	18	5
6	97	68	100 (295)	95	27	12	16	6
7	28	55	13	22	100 (315)	15	13	14
8	23	36	100 (450)	58	45	40	18	3
9	70	52	74	100 (88)	57	6	2	2
10	32	39	40	100 (165)	40	38	45	15

* See footnote TABLE 7, p. 203.

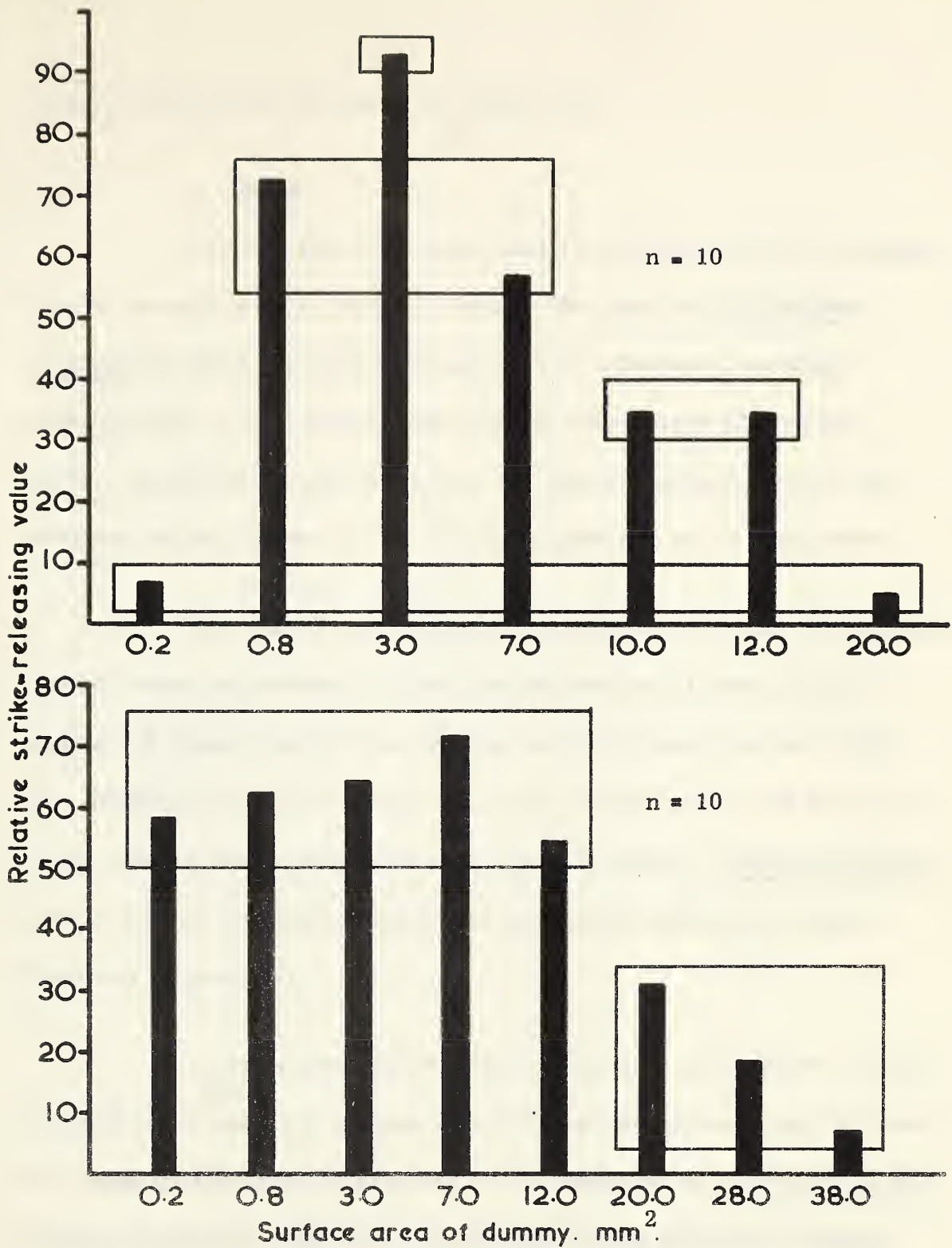


FIG. 40. - The effect of size of dummy prey on the number of strikes made by dragonfly larvae. Upper : *Aeshna interrupta lineata*; Lower : *Libellula quadrimaculata*. There is no significant difference at $P = 0.05$ between values enclosed by the same box.

larger dummies as time went on (Figure 41).

c. Shape

Animals that have specialized prey may initially recognize this by its appearance; such is probably the case with Philanthus triangulum which recognizes honey bees at a distance, although olfactory and tactile stimuli take over at close range (Tinbergen, 1935). Dragonfly larvae, however, are general animal feeders and the form of prey seems to be of little importance in its recognition.

Two sets of experiments, in which the shape of the dummies varied, were performed. In the first experiments (Table 11) the number of arms on a circular dummy varied between one and eight. The dummies were white and were 3 mm. in diameter, and the arms were made of waxed cotton threads 2 mm. in length. Aeshna eremita larvae 35 millimetres in length, did not distinguish between these dummies (Figure 42).

In the second experiments (Table 12), rectangular, square, triangular, circular, X-shaped and Y-shaped dummies of approximately the same surface areas were used. The response of Aeshna eremita larvae, between 35 and 38 mm. in length, to the X- and Y- shaped dummies was significantly less at $P = 0.05$ than the response to the other dummies (Figure 42). Considering the preference for objects that are moving with a fast, jerky rhythm, it may seem strange that

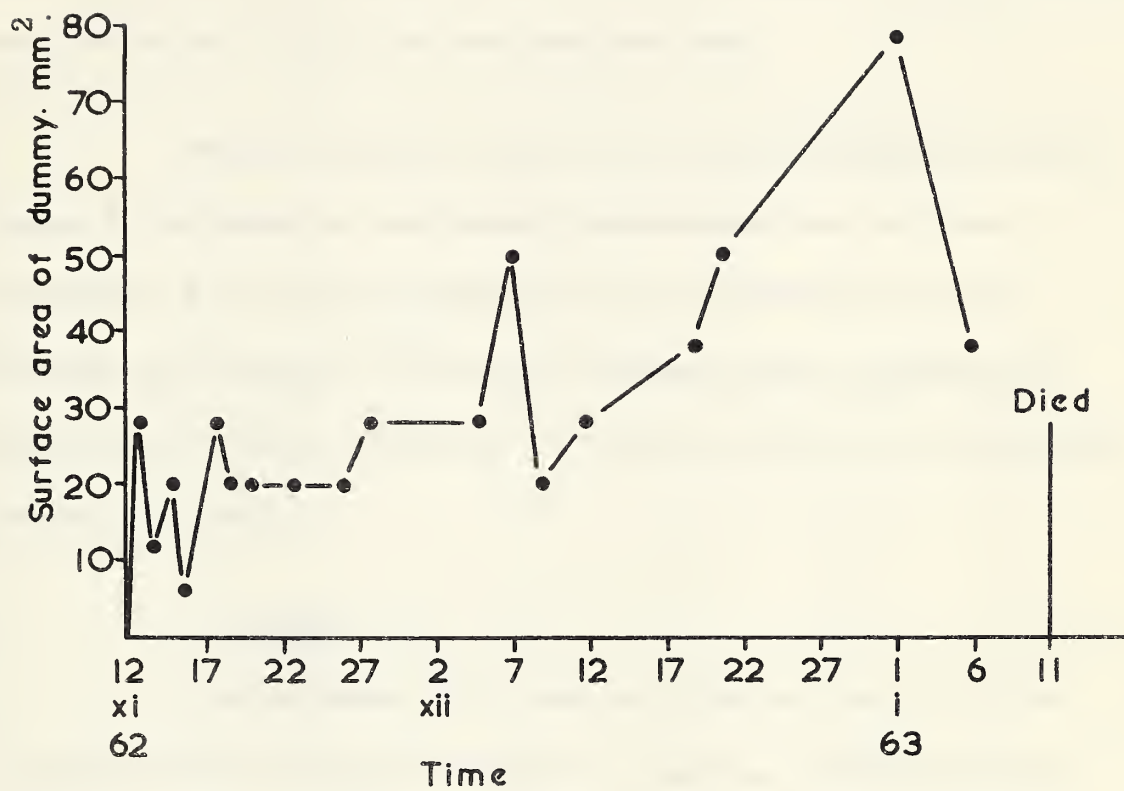


FIG. 41. - The size of the largest dummy that is struck at by a larva of Aeshna interrupta lineata increases with the length of time without food.

the dummies here with the higher flicker-values were not preferred. One possible explanation is that the larvae could not distinguish between the arms of the dummies when they were moving, and the apparent size that was produced was less favourable than the smaller sizes of the more compact dummies. Size, rather than shape, would then have been the factor to which the response was made.

Whether dragonfly larvae can in fact distinguish between shapes is not known as conditioning experiments have not been performed, but it seems unlikely that they discriminate between different prey animals on the basis of shape as such, although the apparent size that the shape may give may be important as a stimulus releasing the strike.

d. Colour

In experiments with coloured dummies, control of the brightness of the dummies is important, and also, especially when dealing with arthropods, the fact that the different colours may reflect different amounts of ultra-violet light should be borne in mind (Carthy, 1958).

Red, green, blue, and black dummies were presented against a white background, and yellow and white dummies were presented against a black background, so that the contrast between the dummies and the background was, to the human eye, approximately

TABLE 11. - The effect of increasing the number of arms on a circular dummy on the number of strikes made by larvae of Aeshna eremita.

Individual	Strike-releasing values of various numbers of arms *							
	1	2	3	4	5	6	7	8
1	45	100 (55)	18	24	29	47	13	31
2	100 (80)	66	48	46	18	26	16	12
3	14	17	51	3	34	100 (35)	11	23
4	100 (30)	100 (30)	40	40	90	73	37	20
5	56	28	44	91	38	100 (32)	56	12
6	64	100 (11)	27	36	64	45	45	9

* See footnote TABLE 7, p. 203.

TABLE 12. - The effect of shape of dummy prey on the number of strikes made by larvae of Aeshna eremita.

Individual	Strike-releasing values of various shapes *					
	●	■	▲	■	✱	Y
1	63	100 (90)	86	39	59	7
2	73	40	100 (15)	87	7	27
3	54	64	64	100 (22)	36	36
4	32	100 (25)	64	24	20	68
5	100 (201)	18	25	9	9	7
6	44	96	96	100 (27)	18	15
7	93	100 (30)	70	87	60	43
8	100 (8)	50	38	38	25	50
9	27	32	57	100 (111)	36	36
10	80	40	60	100 (10)	20	80
11	35	100 (17)	41	53	6	6
12	62	40	22	100 (176)	24	14

* See footnote, TABLE 7, p. 203.

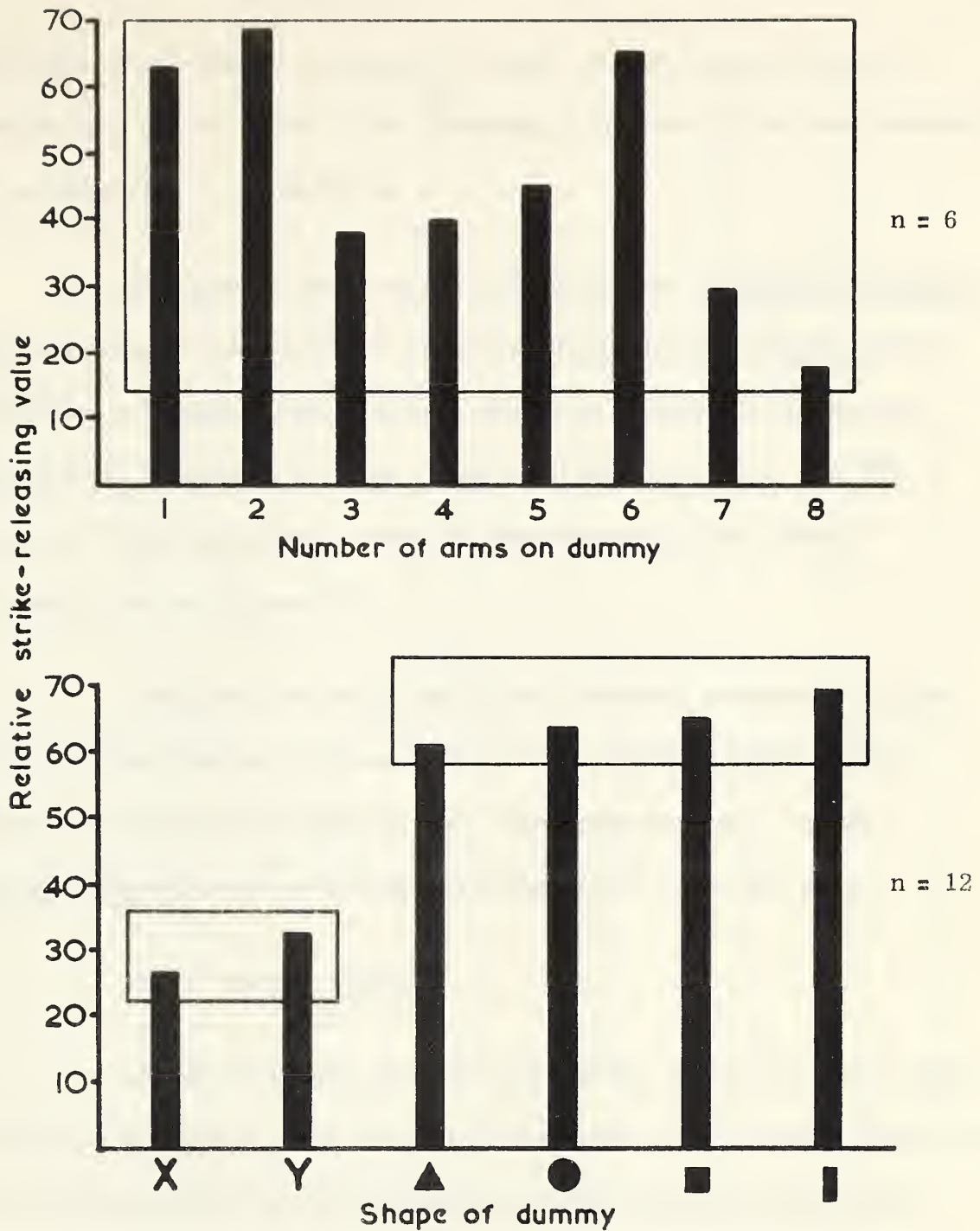


FIG. 42. - The effect of shape of dummy prey on the number of strikes made by larvae of Aeshna eremita.
 There is no significant difference at $P=0.05$ between values enclosed by the same box.

the same in all cases. The spectral output of each dummy was not considered; in view of the close grouping of the results this was probably not an important consideration.

Analyses of the results of experiments on Aeshna interrupta (15 to 17 mm. in length) (Table 13) and on Leucorrhinia proxima (18 to 19 mm. in length) (Table 14) have shown no significant variations between the responses to these colours. It appears, then, that the colour of the prey has little effect on the release of the strike by dragonfly larvae (Figure 43).

Dragonfly larvae probably do, however, possess a limited ability to discriminate between colours since Koehler (1924), using favourable and unfavourable (quinine impregnated) foods, trained Aeshna cyanea larvae to distinguish yellow from violet and grey.

7.43 Tactile stimuli

Alverdes (1924) noted the importance of the antennae in prey capture by Zygoptera, and Richard (1960a, 1960b) has recently confirmed this and has pointed out the importance of mechanical stimuli in the Anisoptera too. In the present study, observations made without knowledge of the work of Richard have further added to our appreciation of the use of tactile stimuli by certain Anisoptera.

When Libellulid larvae and mosquito larvae are placed

TABLE 13. - The effect of colour of dummy prey on the number of strikes made by larvae of Aeshna interrupta lineata.

Individual	Strike-releasing values of various colours *					
	Red	Yellow	Green	Blue	White	Black
1	43	67	58	71	48	100 (21)
2	69	41	100 (49)	65	41	84
3	72	75	50	62	100 (40)	72
4	67	97	93	100 (30)	70	80
5	84	66	89	100 (38)	95	47
6	47	62	84	100 (32)	47	69

* See footnote TABLE 7, p. 203.

TABLE 14. - The effect of colour of dummy prey on the number of strikes made by larvae of Leucorrhinia proxima.

Individual	Strike-releasing values of various colours *					
	Red,	Yellow	Green	Blue	White	Black
1	100 (89)	100 (89)	19	21	45	47
2	100 (69)	45	52	51	45	58
3	17	14	100 (94)	16	52	24
4	100 (51)	17	12	78	8	31
5	25	100 (130)	12	16	72	23
6	52	78	52	37	15	100 (27)
7	100 (79)	96	84	49	14	89
8	10	49	100 (69)	56	72	86
9	79	9	17	100 (160)	46	33
10	100 (52)	33	98	67	33	44
11	100 (31)	45	29	32	32	32
12	83	52	52	17	100 (48)	94

* See footnote TABLE 7, p. 203.

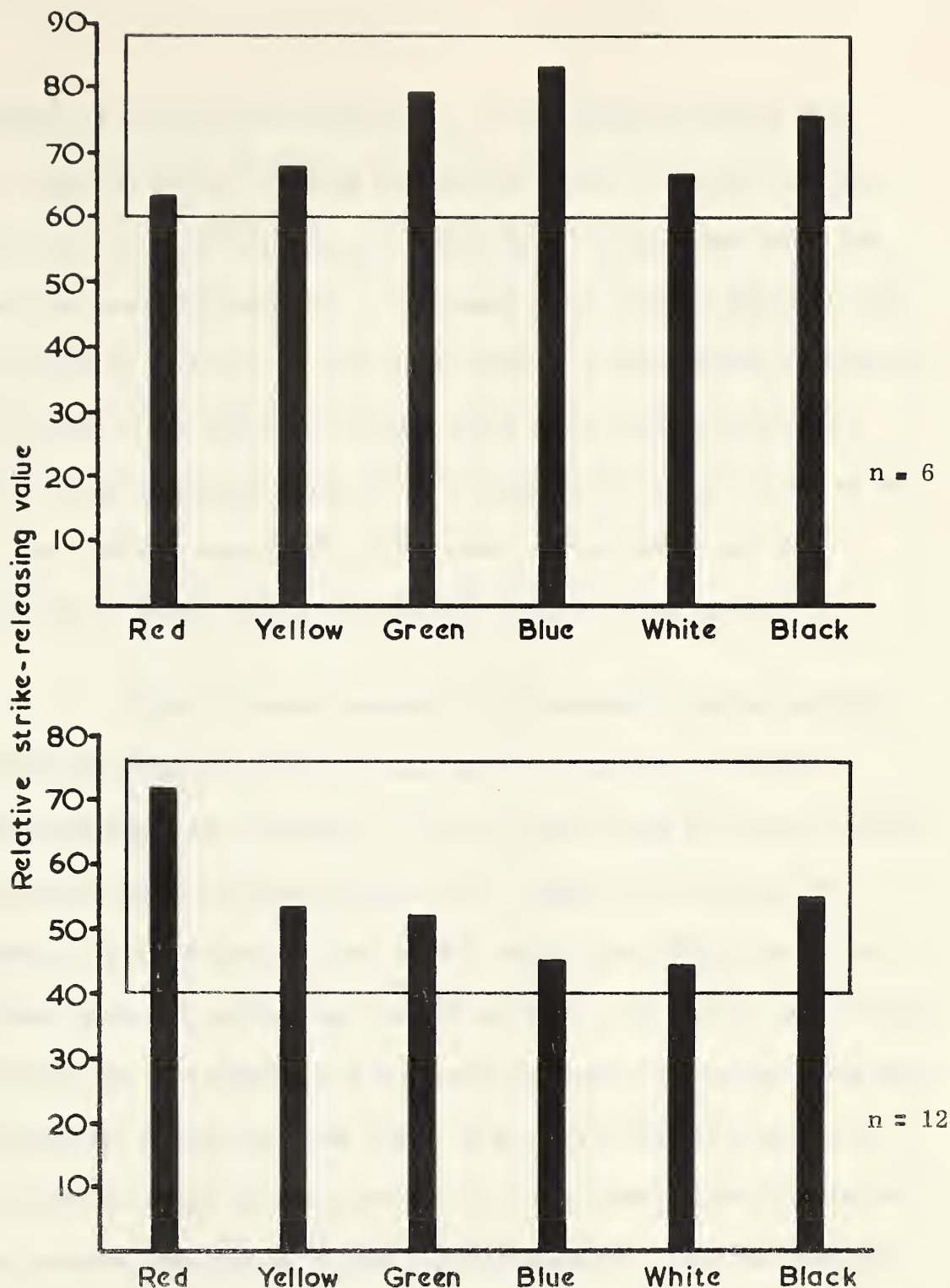


FIG. 43. - The effect of colour of dummy prey on the number of strikes made by dragonfly larvae. Upper : *Aeshna interrupta lineata*; Lower : *Leucorrhinia proxima*. There is no significant difference at $P=0.05$ between the values enclosed by the same box.

together in a dish in the laboratory, it is a common sight to see the dragonfly larvae catching mosquitoes that are browsing on their legs, and the interesting way in which these captures are made has been discussed in Section 7.1. Although most of these prey animals can probably be seen, for the visual field of a dragonfly larva extends well round to the sides, it would at first seem quite probable that tactile stimuli are also important in bringing about the release of the strike. Certain experiments have been carried out to test this hypothesis, using Libellula quadrimaculata as a test animal.

First, a paper dummy was presented to larvae and the number of strikes to satiation was used to estimate the relative effectiveness of two releasers, visual stimuli alone and visual stimuli reinforced by tactile stimulation. For 'visual stimuli alone' the dummy was exhibited in front, above, and to the sides of the larvae without directly touching any part of the body. For 'visual and tactile stimulation', the dummy was frequently brought into contact with parts of the body, particularly the legs. In each of eight experiments on four larvae (Table 15) the response to 'visual and tactile stimulation' was greater than that to 'visual stimulation alone', and the average number of strikes made with the former releaser was significantly greater at $P < 0.001$.

Separate experiments have shown that striking can be

TABLE 15. - Showing the increase in the number of strikes made by Libellula quadrimaculata larvae at dummy prey when visual stimuli are reinforced by tactile stimulation.

Individual	Experiment	Stimulus [†]	Strike-releasing value *
1	i	v	80
		vt	100(40)
2	ii	vt	100(18)
		v	17
	iii	vt	100(116)
		v	85
3	iv	v	40
		vt	100(125)
	v	v	8
		vt	100(52)
4	vi	vt	100(8)
		v	25
	vii	vt	100(185)
		v	68
	viii	v	9
		vt	100(11)

† v = visual stimulation alone ;
vt = visual and tactile stimulation.

* See footnote TABLE 7, p. 203.

reinstigated after satiation by 'visual stimuli alone', by commencing tactile stimulation.

Evidently tactile stimuli are important, but in order to determine whether larvae can react accurately to these stimuli alone, a series of experiments was carried out on larvae which had been blinded by painting over the surfaces of the compound eyes and the ocelli with green 'Pactra Namel' paint. In such insects, accurate strikes were readily released by touching any parts of the legs and the antennae with thin glass rods or cotton threads. On one occasion an apparently well-blinded larva struck at a dummy that was suspended in front of it, although the dummy did not directly touch any part of the body. The movements of the dummy did, however, set up water currents which moved the antennae, and as the larva had not fed for some time the threshold for striking had possibly become so low that these currents were sufficient stimulus to release the strike. More usually stronger tactile stimulation by actual contact with the legs or antennae is needed. Touching other parts of the body such as the dorsal parts of the thorax and abdomen seems to have a higher threshold and does not generally lead to striking.

The use of paraffin wax to stick down the hairs on certain parts of the legs of larvae of Libellula quadrimaculata has shown that the tactile stimuli are received by these hairs. When the hairs on the

legs of the left side of a blinded larva were stuck down, then no reaction could be released by stimulation of this side, although strikes were made to the right, at least to the fore and middle legs. Observations on larvae with normal vision gave even more interesting results, for when the setae on the fore legs were waxed, dummies in contact with these legs would not be struck at even though they could presumably be seen. When the tibiae of one side were waxed, dummies touching those segments would not be struck at, but stimulation of the femora of the same legs generally released the strike.

A further interesting test was performed on Cordulia shurtleffi. A dummy was attached to the end of a waxed thread which was bent so that the thread could touch the mesotibia while the dummy came to lie at the side of the head (Figure 44) and was visible to the larva. If the thread was not touching the leg then the larva stuck at the dummy, but when the thread was in contact with the meso-tibia the larva always struck at this point of contact. Thus, although the sight of the dummy may have been important in releasing the strike its direction was primarily governed by information received from the tactile stimulation.

The large, stout setae on the legs appear to be the important ones for receiving these tactile stimuli, and it is interesting to note that most bottom-living forms that catch prey after tactile stimulation

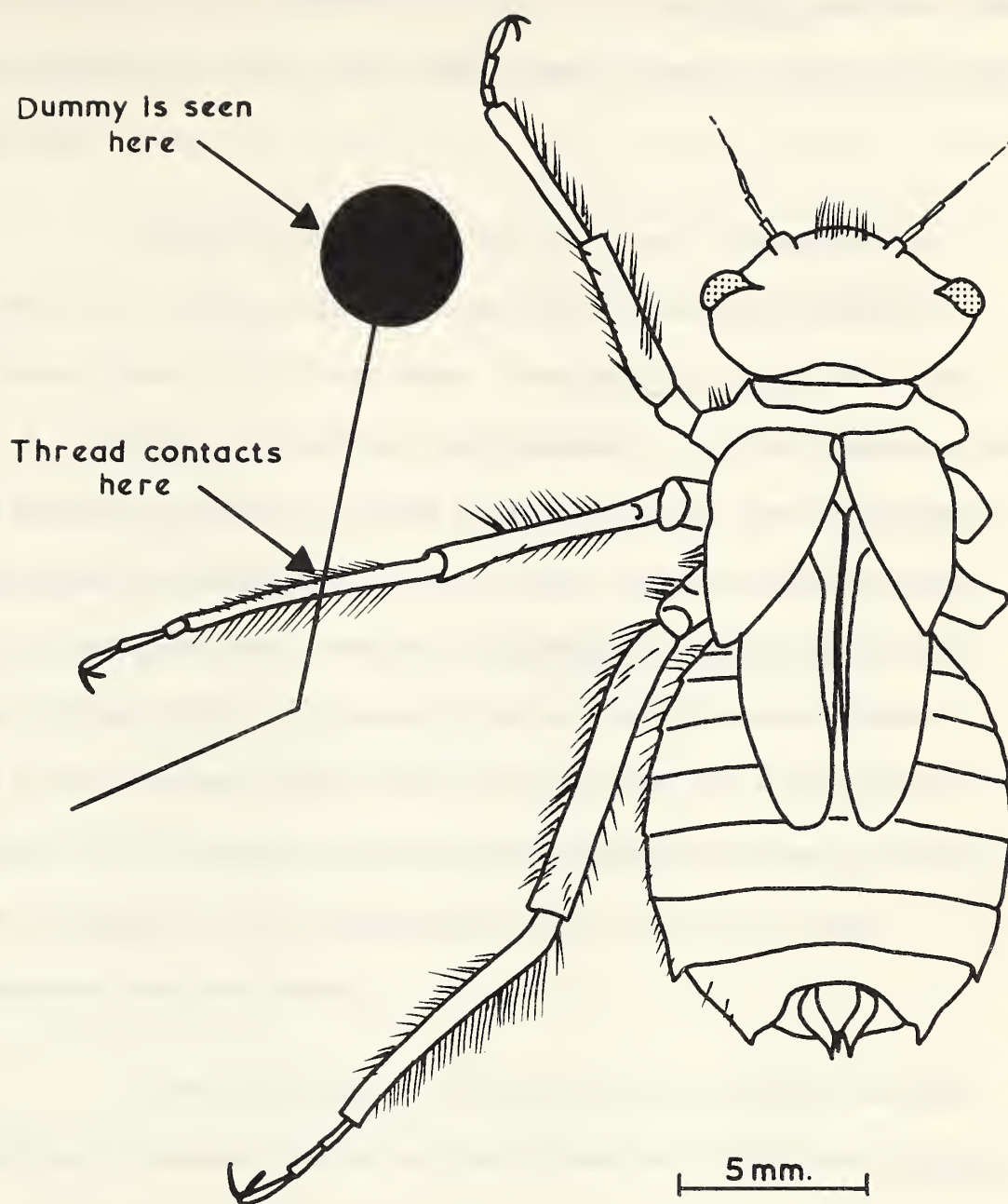


FIG. 44. - Showing the method used to apply tactile stimulation to the meso-tibia of the larva of *Cordulia shurtleffi* and at the same time present a moving dummy in the larva's field of view.

have the legs thickly clothed with setae, whereas Aeshna species, which do not generally react to prey unless they can see it, are more or less glabrous.

This difference in the method of prey capture between Aeshnids and other species has been shown by isolating dragonfly larvae with prey in total darkness. Two Aeshna eremita larvae and two A. canadensis larvae were each confined in complete darkness with ten Zygoptera larvae, two small Libellulid Larvae, two Trichoptera larvae and five Gammarids for three days. At the end of this time nothing had been eaten. But when a Libellula quadrimaculata larva was confined with two Chironomid larvae, five Chaoborine larvae, two Ephemeroptera larvae, five Corixid larvae, three Oligochaete worms, four Coleoptera larvae and five Zygoptera larvae, the only prey animals that were uneaten after three days were a single Zygopteran and one Corixid.

In the laboratory, a response to tactile stimuli has been confirmed in several species of Libellulidae and Corduliidae (Libellula quadrimaculata, Leucorrhinia hudsonica, L. proxima, L. borealis, Sympetrum danae, S. internum, Ladona julia Uhler and Cordulia shurtleffi), but it has not been possible to evoke strikes from normal Aeshna larvae by this means. It would be interesting to examine the behaviour of Gomphid larvae which have a labial structure more like

the Aeshnids but are bottom dwellers and are well clothed in setae like the Libellulids. The unique development of the third antennal segment in the Gomphidae would point to its use as a mechanoreceptor. Certainly larvae of Tanypteryx hageni Selys, a Petalurid which feeds on terrestrial arthropods at night, are known to respond to tactile stimuli (Svihla, 1959).

Although the legs and antennae are the most important parts of the body in the mechanical detection of the movements of prey animals, specialized outgrowths from the heads of certain species may also function as sensory receptors (see Corbet, 1962).

7.44 Chemical stimuli

Aeshnid and Libellulid larvae will strike readily at moving shadows and at objects that are separated from them by glass. Also, an extract of Tenebrio that is released into the water fails to evoke any response even from hungry larvae, and paper dummies soaked in such an extract are no more favourable than untreated dummies.

The olfactory sense thus appears to be of little or no importance in the release of the strike, and Abbott (1925a) similarly concluded that Anax junius was incapable of sensing the chemical nature of a distant object.

There also appears to be no gustatory sampling of the

prey as a preliminary to the release of the strike, for blinded larvae strike equally readily at animate and inanimate objects that are brought into contact with the antennae. The gustatory sense, probably located on the epipharynx, is however important as a test for food after capture (Section 4).

7.5 Discussion

The greater part of the life of a dragonfly larva is spent in performing actions associated with detecting, catching and eating prey. The larval stage has very little dispersal value and it is mainly concerned with growth and development towards the mature adult state. To a dragonfly larva, then, feeding is of prime importance, and forms that have a wide range of food available to them and can detect and catch prey at a distance, will develop more rapidly than those whose ability to exploit the available food is more limited (Corbet, 1962).

We can only speculate as to the methods of detecting and catching prey that were used by the early dragonfly larvae. The behaviour of most modern Zygoptera, that of the primitive Petalurids and of young larvae of all Anisopteran families, suggests that early dragonfly larvae detected prey mainly through the use of mechanoreceptors on the antennae. Since then, the evolution of behaviour has been affected by the specialization of the eyes and by the increase in importance of

mechanoreceptors on other parts of the body.

Evans (1957) has suggested that one way in which natural selection can effect changes in behaviour is to favour a lowering or a raising of the threshold for a particular reaction. This has perhaps been the case with dragonfly larvae. Along with the increased size of the eyes, Aeshna larvae, after the fourth instar, detect prey mainly by visual means and the threshold for a reaction to tactile stimuli has been so raised that only under abnormal conditions, such as the absence of light or during an intense hunger drive, will these stimuli produce a response. In those Corduliids and Libellulids which live permanently amongst trash on the bottom of the habitat, the eyes are not well developed compared with those of Aeshna, and natural selection has favoured an increased susceptibility to tactile stimuli. Whilst still retaining the low threshold for reaction to tactile stimuli, a group of Libellulids, which have left the bottom and taken to climbing amongst vegetation, have developed larger eyes and are able to orientate towards prey in a manner that parallels the behaviour of Aeshna.

The predatory behaviour of dragonfly larvae is innate and there is no evidence to show that the responses to prey in nature are modified by learning during ontogeny. Dragonfly larvae of the genus Aeshna do, however, appear to be capable of a certain amount of learning as shown by the experiments of Koehler (1924) with colours, and Richard (1960a) reports that Aeshna cyanea larvae were able

to associate the human form with food and modified their behaviour accordingly. Abbott (1925b) forced larvae of Aeshna umbrosa to feed in bright light and, after some time, not only did they respond positively to his approach, but also sought out brightly lit areas rather than shaded ones. Abbott (1941) also reports an interesting modification of the behaviour of Gomphid and Libellulid larvae which, when their labia were excised, would swim after food that was presented to them and seize it with their mandibles. Normally, however, there are no such opportunities in nature for behaviour to be permanently modified.

All appetitive behaviour which leads up to the consummatory act of swallowing is, however, plastic and can be adapted to the conditions that prevail. Any part of the behaviour chain may be modified at any time and some may even be omitted depending on the exact configuration of the stimuli that are perceived. For example, the characters shown by prey at a distance lead to the activation of a particular 'Innate Releasing Mechanism' (Tinbergen, 1951) which allows the flow of nervous energy into the appropriate 'Central Excitatory Mechanism'. This CEM is also responsive to inner physiological influences which ultimately determine whether the larva will wait in ambush or will approach the prey. The sudden appearance of prey at close range, however, affects a different IRM and nervous energy is channelled to a different CEM so that the strike may be released immediately without long preliminary orientation or, if

prey is close enough, it may be caught by the labial palps alone without a forward thrust of the labium. After prey is caught, the gustatory and mechanical stimuli that are received from the food determine the action of the mouthparts.

Feeding is not, of course, the only facet of dragonfly larval biology upon which the effects of natural selection have acted. Several other ways in which dragonfly larvae have become adapted to their environments, as well as the importance of this stage in the life cycle as a means of overcoming unfavourable conditions, are all intimately associated with the success of the Odonata since their larvae began to take to water, probably during late Carboniferous times (Tillyard, 1917).

8. PREDATORY BEHAVIOUR OF DRAGONFLY ADULTS

8.1 Behaviour patterns

Feeding by adult dragonflies usually takes place away from water and immature adults may indulge in this activity throughout the day, but feeding by mature individuals, which spend a part of the day in sexual activity over water, is often restricted to early morning and late afternoon. All adult dragonflies catch prey whilst on the wing.

On the basis of their feeding behaviour, adult dragonflies may be classified as 'fliers' or 'perchers'. Most Aeshnids, Cordulegasterids and Corduliids can remain on the wing for long periods of time, and settle only to deal with a large prey animal which they may have caught. Gomphids and Libellulids, on the other hand, spend most of their time perching and they make only temporary flights for prey animals that fly into their vicinity. These innate differences in hunting behaviour do not apparently affect the composition of the food or the success with which it is caught, but they have important effects in other ways. Large flying forms are able to maintain a high body temperature and may remain active after low temperatures have forced perchers to retire. Such large forms, particularly Aeshnids, are the first to be flying in the morning and they remain on the wing longer in the evening than do smaller species. At Flatbush in July and August 1962, Sympetrum spp. did not fly in the mornings until the temperature

rose to 17°C. In the evening these small perching forms were generally not seen on the wing after the temperature had dropped to 18°C. But Aeshna eremita was regularly seen flying in the early morning when the temperature was only 14°C., and this and other species of Aeshna, Cordulia shurtleffi and Tetragoneuria spinigera were often seen flying at dusk when the temperature had dropped below 16°C. and the light intensity was low. But perching forms, besides conserving energy, can change their positions and choose their substrates to take advantage of the sun's radiation or remain active at temperatures which are too high for fliers.

Wind affects both fliers and perchers, but the large fliers are able to combat quite strong gusts and remain airborne with reasonable control. Small perchers stay close to the ground under such conditions, using patches of bare ground as supports rather than remaining on swaying herbage. Prey that is caught at these times is probably being blown by the wind.

Fliers tend to hunt back and forth along a fairly regular beat in active search for prey. They often seem to use a landmark to define their path, such as a clearing in a forest, the tops of trees, the edge of a forest, or the border of a pond. Deviations are made from these regular beats in order to catch prey, but the predator usually returns to its original path. The limits of the feeding area are often defined

by meetings with other dragonflies, although these are rarely of a truly aggressive nature.

Perchers do not search for prey, but remain in ambush on their supports and only take to the air when prey is detected. These forms may perch on the ground, in bushes or on any other suitable support, although the smaller species tend to use grasses and other low herbage. The usual position is a horizontal one (Figures 45a and 45b), the long hind legs being important in taking the weight of the body. Occasionally an oblique perch (Figure 45c) is seen and the orientation of this may be determined by the direction or intensity of the sun's radiation. It is important, however, that the large facets in the upper parts of the eyes are directed upwards, for it is with these that prey is best detected. Whilst on the perch, the body is held perfectly still except for the head, which is occasionally jerked from side to side. It is not clear whether these movements are for the purpose of following prey or are a form of cleaning activity. The eyes and mouthparts are often cleaned by the forelegs, the flattened spines on the tibiae probably being of particular importance here. Often the forelegs remain still whilst the head moves between them. The wings of a perched dragonfly in ambush are usually held slightly forward and somewhat depressed, in which position they shade the thorax and perhaps are also in a good position for rapid take-off.

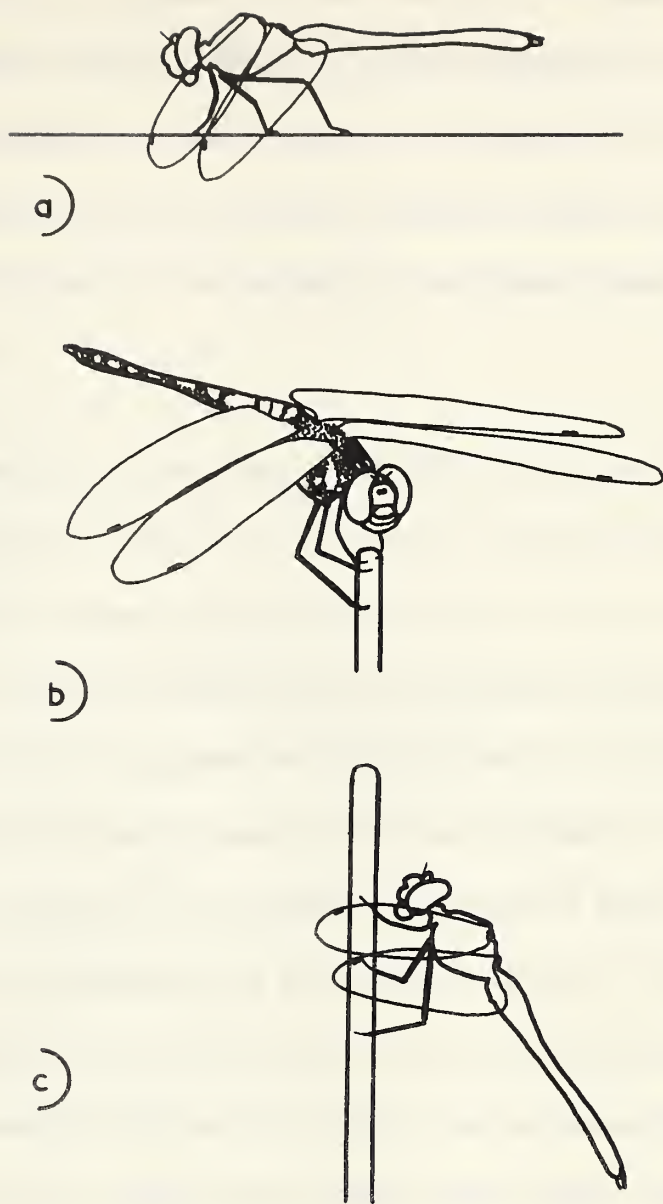


FIG. 45. - Perching positions of Sympetrum danae.

When prey is sighted, the percher type of dragonfly quickly takes to the air, often performs some complex aerobatics to catch its prey, and returns to its perch within a few seconds. The same perch is often used as a base for several captures, just as a male Libellulid, engaged in territorial behaviour over water, tends to favour a particular perch.

The characters and roles of the different parts of the eye have been discussed in Section 3.2. Prey is usually detected above the head and the large ommatidia, which in many forms function superpositionally, are well constructed for discerning movement especially when the prey is silhouetted against the sky. Tirala (1923) experimented with small paper pellets and decided that, where the object is not too large, it is the speed with which it moves and not its shape which is important as the initial stimulus. But as the dragonfly approaches its prey and moves into a prey catching position, the object will be seen by the smaller antero-ventral ommatidia, where the visual acuity is high and the shape of the object may be discerned. I have often seen dragonflies fly after large insects, but turn away before they reached them, and at the Totem Pond in 1961 airborne seeds of Typha latifolia were good attractants for prey-catching Aeshna interrupta lineata, but again they always veered away after the seeds had been seen at close range. In Uganda, Pantala flavescens has been seen to fly after Macrotermes but turn away at

the last moment, probably because these insects were too large to qualify as prey (Corbet, 1962; personal communication). Baldus (1924) was successful in getting Aeshna adults to turn towards paper pellets, but noted that the dragonflies turned away when the image of the pellet was perceived. It would be difficult to decide what characters of a dummy would make it most acceptable as prey, but it certainly seems that adult dragonflies are more selective in the objects that they will attack than are the larval counterparts, to which shape and contour are of little or no importance.

It is generally asserted that prey capture is always effected by the spiny leg basket which is conveniently placed beneath the mouth. The capture of large prey animals by this method, although very fast, can often be clearly seen, but the transfer of prey to the mouth is not as obvious. When the prey is very small, as is usually the case (Section 6), the details of prey capture cannot be followed accurately by the unaided eye, and all that is usually seen is a rapid transient lowering of the legs. This fleeting action infers that small prey is also caught by the legs, but it would be most interesting to see just how such small insects are handled and transferred to the mouth. Good cinematography would be invaluable, but in order to show the required detail, many technical problems need to be solved. Pajunen (1962) has obtained motion pictures recording the aggressive behaviour patterns of Leucorrhinia dubia van der Lind, but pictures designed to

show the handling of small prey animals by the legs of the dragonfly pose greater difficulties than this. Until such records are obtained we can only speculate on the capture of small prey and its transfer to the mouth.

It is possible that only the front legs function in catching small prey. When these legs hang down together, the spines of the inner rows on each tibia overlap (Figure 46) and, with the spines of the outer rows, a scoop-like arrangement is formed. The prey is not necessarily impaled on the spines nor is it grasped by them, but is held against them by the forward movement of the legs as they fold forwards at the coxo-trochanteral and femoro-tibial joints. The scooping movement used to catch the prey is then continued forwards and upwards to the mouthparts, where the labium is dropped so allowing the prey to be taken by the mandibles. Small prey is quickly chewed and may be consumed in flight, although many perchers will return to their perch before they have completed the meal. The labium serves to contain the prey after it has left the legs.

Larger prey animals cannot be scooped out of the air in this manner and all six legs may be used to effect the catch. The spines on all of the legs are then used to maintain a firm grip on the capture and prevent its escape. The transfer of prey to the mouthparts follows immediately after capture and appears to be completed in a single jerky movement. Large Aeshnids may be able to consume such prey whilst in flight, but usually dragonflies fly away from the feeding ground to the

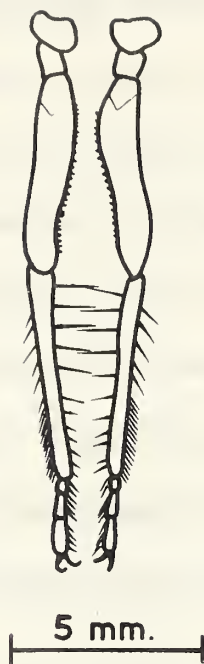


FIG. 46. - Anterior view of the fore legs of Aeshna interrupta lineata in prey catching position.

nearest support, where they settle in a vertical position and take their meal more leisurely. At Flatbush I have seen Aeshna eremita catching Zygoptera over water and then flying to the bush to complete their meals. And similarly Cordulia shurtleffi, another species that can remain on the wing for long periods at a time, would settle to eat smaller Anisoptera and Zygoptera, and on one occasion an individual of this species settled on a shirt hanging on a line in order to consume a Chrysopid. On June 1st 1962, the same species was observed catching large, newly emerged Limnephilids and then flying to the nearest trees to eat their captures. When carrying such large prey in their mouths, dragonflies become 'head-heavy'; their flight is jerky and they lose much of their manoeuvrability and can often be caught by hand.

The prey does not have to be flying in order to be attractive to dragonflies, and, although commoner in the Zygoptera (see Balfour-Browne, 1909), there are several records of Anisoptera picking up stationary prey from vegetation. On August 13th 1962, I observed several Aeshna eremita searching amongst the Carex along the border of Scaup Lake and catching Zygoptera. Many damselflies were plucked off the vegetation and sometimes a pair of damselflies in tandem would be caught together. The Aeshnids had to hover, wings beating against the vegetation in order to perform this feat. In addition, other damselflies were caught in flight, often after having taken to the air because of the disturbance caused by the hunting Aeshnids.

The capture of resting prey adds weight to the hypothesis that dragonflies see shapes well and may be attracted solely by these characters of their prey. Resting prey will be seen by the ventral ommatidia where the resolving power is high and appreciation of the finer details of objects is greater.

The feeding by dragonflies on an aggregation of prey animals has been discussed at length by Corbet (1962), and need not be dealt with in detail here, except to add a few examples.

Cordulia shurtleffi was one of the earliest dragonflies to emerge at Flatbush in 1962, and this species had been flying for five days when a large emergence of Zygoptera began from Scaup Lake on May 31st. For several days after, large numbers of C. shurtleffi were regularly seen catching these newly emerged damselflies which flew awkwardly away from the water. When the peak of emergence was over, the numbers of C. shurtleffi feeding in this area diminished.

Wesenberg-Lund (1913) reports Aeshna grandis following running horses and seizing their prey from the fly swarm around the horses' noses. At Flatbush, the swarm of Simuliids that would accumulate around one's head, were often preyed upon by large numbers of Cordulia shurtleffi and Tetragoneuria spinigera at the same time. And on August 5th 1962, a large gathering of people attracted swarms of Simuliids and Culicids, which in turn provided food for many

Aeshna eremita and Aeshna canadensis. Lamborn (1916) noted how Orthetrum chrysostigma would follow humans and catch tse-tse flies that settled on their backs, and there are other examples from Africa of Anisopterans following animals (see Corbet, 1962).

The feeding and sexual phases of behaviour are generally temporally and spatially separated, the former occurring in early morning and late afternoon away from water, whilst sexual behaviour usually occurs at the warmer times of the day and over water. Female dragonflies go to water only for mating and oviposition. Male dragonflies holding territories over water do not feed to any great extent, but fly continually over the area (fliers) or inspect their domain from a central perch (perchers) with occasional tours of inspection. Intruding dragonflies are driven away or mated with. But when feeding, other dragonflies are largely ignored and males and females of several species may feed communally on a large swarm, or use the same area to feed on more dispersed prey.

The time spent in these two activities also varies according to the age of the dragonflies. Feeding is dominant in immature and in old individuals and may take place at all times of day and even over water. At the Totem Pond in August 1961 old Aeshna interrupta lineata were regularly seen feeding over water, and Aeshna eremita has been seen feeding on Zygoptera in August and Aeshna umbrosa on emerging mayflies

in September, both over water. At each of these times there were many individuals in a small area and although the dragonflies made many flights at each other, these would never result in actual clashes; the 'attacker' often flew off, leaving the 'intruder' to pursue its previous path, a situation that would not be expected if the sexual drives were strong. Light intensity may act to suppress reproductive behaviour of mature individuals in the earlier and later parts of the day or, as Corbet (1962) has suggested, at the times when males and females have been seen feeding together, the air temperatures may have been below the threshold for reproductive behaviour.

8.2 Discussion

The study of adult feeding behaviour is hampered by the speed and relative inaccessibility of the insects under study. Most of the prey is very small and the finer details of prey capture cannot be followed accurately.

It appears, however, that before the capture is made more information about the prey is required than is the case in larval dragonflies. The eyes of the adults are considerably better developed than are those of the larvae and it seems certain that they can discern shapes well. Many larval forms depend to a large extent on tactile stimulation in order to detect the presence of potential prey, and unless the

stimulation is too great any moving object can bring about the release of the strike. Even when orientating visually, larvae respond only to size and movement. Adult dragonflies, too, respond at first to movements and size of prey, but as they come closer they are able to receive information about other characters, and these will decide whether the initially attractive object is caught or left alone. The nature of these other characters is not known, but the movements of the legs and wings of the prey, with their increased flicker values, are no doubt of some importance.

The evolution of feeding behaviour in adult dragonflies has probably been in a direction involving less dependence on land. Perhaps adult dragonflies originally settled close to their prey and caught it directly with the mouthparts. Later, as the legs moved forwards and manoeuvrability in flight increased, resting prey could be picked off by the legs of a flying dragonfly in a way similar to that in which Asilids catch prey. The action was then much quicker and more elusive prey could be caught. The skewness of the thorax is probably a very old character and the capture of prey by the legs is doubtless of the same age. But the hyper-development of the eyes, leading to their meeting on top of the head, is a comparatively recent development (Fraser, 1957), and it is possible that the present-day condition, where almost all prey is caught in the air, was not attained until the eyes had reached such a size that prey could be detected over a wide area. At the present time,

the structural adaptations have reached such a state that the large insect population of the air can be successfully taken advantage of, and occasional observations of Anisoptera picking up stationary prey show a reversion to a form of behaviour that was previously more common.

The distinction between fliers and perchers probably represents a dichotomy in the path of evolution, both types having evolved independently after the capacity to pick up prey with the legs had developed. It is interesting to note that Aeshnids, both as larvae and adults, search for their prey more than do other forms, which rely more on ambush in both stages.

9. DISCUSSION

The Odonate larva probably first became dependent on water during the Upper Carboniferous when swamps covered large areas of the world and giant Meganeisoptera ruled the air. In Permian times larvae probably spent as much time in the water as they did out, although adaptations to an aquatic existence, principally in the form of gills, must have been well developed. Having taken to water via the muddy shores of primeval lakes, these dragonfly larvae were, no doubt, bottom dwellers which sprawled amongst mud and debris in shallow water; their eyes were small and prey was detected by the use of mechanoreceptors on the antennae. Since that time certain groups have left the bottom and adopted the habit of climbing amongst aquatic vegetation, whilst others have taken to burrowing.

The main Zygopteran line had arisen by the Upper Permian and the first Anisopteran fossils are found in Jurassic rocks. Most modern Zygopteran larvae are weed-dwellers, but Anisopteran larvae have occupied a variety of niches. Petalurids are the most archaic Anisoptera; their larvae live in the vicinity of highland streams and have retained the habit of their Permian ancestors of leaving the water at times and leading a terrestrial existence. The Aeshnidae in general have adopted the climbing habit and their eyes have become enlarged so increasing the area over which prey can be detected. The

remaining, more recent, families have become adapted to all three habits - burrowing, sprawling and climbing. Gomphids are either burrowers or sprawlers, whilst Cordulegasterid larvae burrow into soft mud or sand. Libelluloids are sprawlers on the whole, living amongst loose sand, mud or leafy trash, but one group of Libellulid larvae has taken a new line characterized by an increase in the size of the eyes and the habit of climbing amongst vegetation. This increase in the size of the eyes has thus evolved twice within the Anisoptera.

We may distinguish two types of predatory behaviour of dragonfly larvae, depending on whether they live at the bottom and detect prey by tactile and visual means, or whether they climb amongst vegetation and depend mainly on visual stimulation for the detection of prey and orientation towards it. The first group includes the Petalurids, Gomphids, Cordulegasterids, and the sprawling Libelluloidea. Its members have small but often protruding eyes and setae cover the body and legs, and they are rather inactive. They usually wait in ambush for prey to come to them, for it is detected mainly by mechanical stimuli which are ineffective at a distance. Thus, when prey is detected it is close at hand and there is little time for careful orientation, and Libelluloid larvae have the remarkable ability of being able to turn only the head and thorax towards the prey and then release a rapid strike.

The climbing forms have large eyes and they are more

active than the sprawlers and burrowers. They quite readily use 'jet-propulsion', expelling water from the anus, and they often stalk prey. This group is best typified by the Aeshnids which depend entirely on their eyes for orientation towards prey in daylight. Since they can cover a larger field by reason of their good vision and tendency to leave ambush and stalk, a greater amount of food is available to them than to species which have poor vision and stay in ambush. Climbers detect prey at a distance and stealthy orientation can usually be accomplished and indeed is often necessary since Aeshnids cannot turn their heads alone towards prey. It must therefore be directly in front of the dragonfly larva before an accurate strike can be released. If prey is first detected when it is close but out of the mid line, the predator must turn its whole body, a process which is slow and also disturbing to the prey. I have no evidence that Aeshnids can feed in darkness when the eyes would be ineffective. If prey is caught under such conditions tactile stimulation is probably important.

A group of Libellulids, including species of Sympetrum and Leucorrhinia, has left the bottom and adopted the climbing habit; their eyes are larger relative to the size of the head than most Libellulids although they have retained the ability to react quickly and accurately to tactile stimuli. It is difficult to decide whether the predominantly-tactile or the predominantly-visual method is the more successful, but the versatility in behaviour of Sympetrum must have added in no

small measure to their success.

The mode of life of a dragonfly larva affects the composition of its diet. Weed-dwelling species eat a wider range of prey than do sprawling and burrowing species, because they take prey at all levels from the water surface to the substrate. Prey which spends much or all of its time at the surface (i.e. air-breathing species) is largely denied to bottom dwellers but readily available to climbers.

The labium of the larval dragonfly is often said to be a marked adaptation to life in water. It can, however, be used out of water for I have seen starved Aeshna interrupta lineata larvae climb up supports and use the labium to catch dummy prey in the air. A study of the action of the labium in terrestrial larvae of Megalagrion in the Hawaiian Islands would be useful. The condition of the labium before Odonate larvae took to the water is not known, and the evolution of its present-day form is difficult to envisage (see Snodgrass, 1954).

In the Aeshnidae, Gomphidae, and Petaluridae, the labium is more or less flat, though it tends towards concavity in the latter family. In the Cordulegasteridae and the Libelluloidea, the labium is deeply concave and, at rest, the labial palps cover the lower parts of the front and sides of the head. Both types of labium are found in climbers, in sprawlers, and in burrowers. Amongst the climbers,

Aeshnids have a flat labium whilst Sympetrum has the concave type; sprawling Libellulids and burrowing Cordulegasterids have concave labia whereas sprawling and burrowing Gomphids have flat ones. Both types, then, function well in all microhabitats. The large labial palps of Libelluloids confer certain advantages to their possessors, which are, incidentally, the most recent families in the suborder, but the sharp palps of Aeshnids are more useful in other ways. Small and elusive prey can usually be better contained by the concave type of labium, because long palpal setae are able to form a roof over the cavity formed by the palps and the prementum. But the small, short type of palp is better fitted for holding and piercing large prey.

The dragonfly larva feeds in this way until it is ready to transform to the adult stage. It now leaves the water and there emerges an insect which is as well adapted to an aerial existence as its larva was to an aquatic one. As Snodgrass has said (1954): "The metamorphosis of the dragonfly's head gives us a striking example of how a major part of an insect can be structurally modified in two different ways to serve the needs of the insect in two different phases of its life."

The eyes of the adult are very large relative to the head, irrespective of their size in the larva; they are widely separated on top of the head of Gomphids, but less separated in Petalurids and Cordulegasterids, and confluent for some distance in the other families. The facets are largest in the dorsal part of the eye,

diminishing in size towards the antero-ventral region. In larvae too, there is a similar distribution of facet diameters, but the ommatidial angles in the antero-ventral region of the eye of the larva are considerably larger than those in the same region of the adult. This perhaps explains the fact that only the size and movement of prey are important to larvae, whereas adults, which are initially attracted by these two characters, select prey on the basis of its shape. In both stages, however, the eyes are well fitted for their use; they command wide fields of view, there are large and small facets for detection and fixation respectively, and there are areas of binocular vision above, in front, and below the head.

A further correlation between the morphology of the eye and predatory behaviour is found in the distinction in size between the upper and lower facets and the method of hunting by dragonfly adults. The average ratio of size of large and small facets is 2.7 in Gomphids, 2.1 in Libellulids, 1.8 in Macromids and Corduliids, 1.7 in Cordulegasterids, and 1.7 in Aeshnids (Lew, 1937). Furthermore, the large ommatidia in Gomphids and Libelluloids are unpigmented and function superpositionally. Most members of these last two groups are perchers, that is, they wait in ambush for prey to come into their vicinity, they fly up and catch it, and then return to their perch. Prey is always detected above the head and this area is covered by large, unpigmented ommatidia, which are excellent for

discerning movement, on account of the great luminosity of the image perceived by them. Cordulegasterids and Aeshnids, however, are fliers, hunting on the wing with no particular orientation to the direction in which prey will appear, although it is often sighted from below. The ratio of the size of large and small ommatidia is less than it is in perchers and all ommatidia function appositionally.

After metamorphosis the labium is no longer extensible but is modified to suit the needs of an adult which catches and consumes prey on the wing. It plays no part in the initial capture of prey for the legs have forgone their function as locomotory organs and are modified for taking prey in the air. Here there is a need for the prey, once caught, to be contained until it can be swallowed, and the labium fulfils these requirements. Its sclerites, especially the palps, are broad and flat and they effectively enclose the other mouthparts below, behind, and at the sides, whilst the labrum prevents the escape of prey in front. The available muscles serve to increase the cup-like form of the labium, and when relaxed it drops back allowing more food to be taken in.

In the adult there are two types of labium which correspond to the two larval types. In the Libelluloid families the movable hook is absent and the palps are large and meet in the mid-line, whilst in the other families the movable hook is present and the palps are not so large that they completely overlap the median lobe. Although modified, the adult labium retains many larval characters such as

the dentate border to the lateral lobe in Cordulegaster. It is difficult to decide whether the distinctions in the structure of the labium between families have arisen in response to its use in the larva or the adult. Adaptations by both stages have affected the evolution of the Odonata, but the profound influence of the ethology and ecology of the larval stage has often not been given due recognition, especially because the adult wing venation provides the best single character for the identification of dragonflies.

It has not been the purpose of this study to attempt to relate the various aspects of predation by dragonflies to the accepted classification of the Anisoptera, and, indeed, it would probably not be possible to get very far with this pursuit. It has, however, often been found appropriate to point out differences in the methods of feeding between certain families and genera. Although we think mainly in terms of morphological characters when distinguishing between members of a given category, other characters, such as those ethological and ecological, can often be very informative and certainly interesting, as Evans' study (1957) on the genus Bembix has shown. Our understanding of the evolution of dragonflies can perhaps be better understood by detailed comparative studies of their behaviour and ecology, and if these conform to and hence support taxonomic concepts of the group, so much the better.

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APPENDIX

A list of Anisoptera found in the study area during 1962 with the dates on which the adults were first seen

Gomphidae.

<u>Ophiogomphus colubrinus</u> Selys	12.vi
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Aeshnidae.

<u>Aeshna canadensis</u> Walker	30.vi
<u>Aeshna eremita</u> Scudder	17.vi
<u>Aeshna interrupta lineata</u> Walker	8.vii
<u>Aeshna juncea</u> L.	19.vi
<u>Aeshna sitchensis</u> Hagen	15.viii
<u>Aeshna umbrosa</u> Walker	11.viii

Corduliidae.

<u>Cordulia shurtleffi</u> Scudder	26.v
<u>Tetragoneuria spinigera</u> Selys	4.vi

Libellulidae.

<u>Ladona julia</u> Uhler	1.vi
<u>Leucorrhinia borealis</u> Hagen	23.v

Libellulidae (cont'd.)

<u>Leucorrhinia</u> <u>glacialis</u> Hagen	30.v
<u>Leucorrhinia</u> <u>hudsonica</u> Selys	21.v
<u>Leucorrhinia</u> <u>proxima</u> Calvert	29.v
<u>Libellula</u> <u>quadrimaculata</u> L.	4.vi
<u>Sympetrum</u> <u>costiferum</u> Hagen	11.viii
<u>Sympetrum</u> <u>danae</u> Sulzer	30.vii
<u>Sympetrum</u> <u>internum</u> Montgomery	26.vi
<u>Sympetrum</u> <u>madidum</u> Hagen	15.viii
<u>Sympetrum</u> <u>obtrusum</u> Hagen	29.vi
<u>Tarnetrum</u> <u>corruptum</u> (Hagen)	?

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